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THE FEMALE GENITALIA OF THE HETEROPTERA: MORPHOLOGY AND BEARING ON CLASSIFICATION[1]

By G. G. E. Scudder

(*Department of Zoology, University of British Columbia, Canada.*)

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With 103 Text-figures

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[1] Part of a dissertation presented in partial fulfilment of the Degree of Doctor of Philosophy in the University of Oxford.

I. Introduction

Dupuis and Carvalho (1956) have given a general account of the structure of the female genitalia in the Heteroptera. Elsewhere (Scudder, 1957*e*, 1957*f*, 1959), I have given a new interpretation of the ovipositor in the Hemiptera. This scheme is followed here.

The musculature of most of the British families has been examined and that of six is figured here, though not described in detail, the labelling being self explanatory. Larsén (1938) has studied the musculature in the aquatic Heteroptera. The musculature has been very useful in confirming homologies. Only muscles associated with and affecting the interpretation of the female genitalia are here labelled.

The value of the female genitalia in the systematics of the group is considered. In the text, families are placed in superfamilies on the basis of the structure of the female genitalia. This is *not* an attempt to erect a system of classification on this evidence alone, but is adopted for simplicity in presentation, so that the results may be assessed easily by other workers who might wish to use this morphological study in further systematic work. Usually, however, the arrangement agrees with established custom. Where this is otherwise, a discussion is given.

The spermatheca in the Heteroptera has been described and discussed by Pendergrast (1957) and will not be treated in detail here. However, some additional information on this organ in some families has been obtained and so is described and discussed in the appropriate places in the text.

II. Material and Methods

The female genitalia were examined from dried museum material after the abdomen had been removed from the specimen and boiled in 10 per cent. potassium hydroxide solution. Material was passed through glacial acetic acid, stained in acid fuchsin and cleared in beechwood creosote. The musculature was studied from dissections of fresh material. Specimens were dissected under 50 per cent. alcohol immediately after having been killed in ethyl acetate vapour.

All drawings were made by using a squared graticule eyepiece. The drawings are not to scale.

III. Some Aspects of the General Structure

The female genitalia of the Heteroptera may be homologised with the structure seen in the Lepismidae (Thysanura) (Scudder, 1957*e*, 1957*f*). The terminology in this paper follows the scheme proposed by Scudder (1957*f*).

The ovipositor is situated on abdominal segments VIII and IX. The ventrolateral parts of tergum VIII are often separated from the median part, as separate sclerites, paratergites VIII, which carry spiracles VIII. Ventrolaterally on either side of segment VIII, beneath the paratergite, is located a basal sclerite or first gonocoxa. This carries ventrally and caudally the first gonapophysis. The dorsal edge of the latter is heavily sclerotized and forms the grooved first ramus. This ramus is often produced anteriorly beyond the

base of the first gonapophysis internally. Segment IX carries a pair of second gonocoxae, to which are attached a pair of second gonapophyses. The ventral edge of each second gonapophysis is heavily sclerotized and forms the ridged second ramus ; this interlocks with the first ramus. Attached to the internal part of the first gonapophysis or to the base of the first ramus is the gonangulum. In the Heteroptera and the other Hemipteroid groups, the gonangulum is fused posteriorly to tergum IX. It is triangular or often $\wedge$-shaped. The anterior limb or edge of this sclerite is the part fusing with the first ramus or gonapophysis. The posterior limb or side is fused either partially or completely with tergum IX. The ventral angle of the posterior side or limb articulates near the mid-point of the dorsal edge of the second gonocoxa. This articulation forms the fulcrum on which the second gonocoxa pivots and is rocked by opposing muscles (figs. 98–103, 1 and 3). The extensor muscle of the gonapophyses (muscle 1) is attached to the posterior part of the second gonocoxa, behind the fulcrum, and the retractor muscle of the second gonapophysis (muscle 3) is attached to the anterior part of the second gonocoxa, anterior to the fulcrum.

A characteristic feature of the Heteroptera is the difference in shape and size of the two pairs of gonocoxae. The second gonocoxae are more slender than the first pair.

The structure called the " outer ramus of the first valvula " and labelled rivlo, by Snodgrass (1933), has caused some confusion. Snodgrass regards the first gonapophysis (= first valvula) as possessing two rami, an inner and an outer. The inner is a sclerotization of and prolongation of the first gonapophysis, to which is attached the gonangulum : this is here termed the first ramus and interlocks with the second ramus which is part of the second gonapophysis and connects it with the second gonocoxa. The " outer ramus " of the first gonapophysis is not an analogous structure, but a thickened sclerotization of the ventral edge of the first gonapophysis. It is the theoretical homologue of the second ramus, but does not connect the first gonapophysis to the first gonocoxa. The first ramus is without a homologue on the second genital segment. Whilst the first and second rami are analogous, they cannot be regarded as homologous structures.

IV. Arrangement of Families and Superfamilies as Suggested by the Female Genitalia, Excluding the Spermatheca

Pentatomoidea
- Cydnidae
- Urostylidae
- Brachyplatidae
- Scutelleridae
- Canopidae
- Tessarotomidae
- Acanthosomidae
- Dinidoridae
- Eumenotidae
- Pentatomidae

Pyrrhocoroidea
- Pyrrhocoridae

Coreoidea
- Coreidae
- Colobathristidae
- Rhopalidae
- Alydidae

Lygaeoidea
- Lygaeidae
- Stenocephalidae
- Largidae
- Berytinidae
- Piesmidae

Aradoidea
- Aradidae
- Dysodiidae

Cimicoidea
- Nabidae
- Velocipedidae
- Miridae
- Isometopidae
- Anthocoridae
- Cimicidae
- Microphysidae
- Thaumastocoridae
- Polyctenidae

Dipsocoroidea
- Dipsocoridae

Reduvioidea
- Reduviidae
- Phymatidae

Tingoidea
- Tingidae
- Vianaididae

Saldoidea
- Saldidae
- Leptopodidae
- Mesoveliidae

Gerroidea
- Veliidae
- Hebroveliidae
- Macroveliidae
- Gerridae
- Hydrometridae
- Hebridae

Nepoidea
- Nepidae
- Belostomatidae

Naucoroidea
- Naucoridae
- Aphelocheiridae

Notonectoidea
- Notonectidae
- Pleidae

Ochteroidea
- Ochteridae

Corixoidea
- Corixidae

Incertae sedis I
- Leotichidae
- Helotrephidae
- Galgulidae

Incertae sedis II
- Aneuridae
- Enicocephalidae
- Schizopteridae
- Termitaphididae
- Joppeicidae

V. Systematic Consideration of the Female Genitalia of the Families and Superfamilies of Heteroptera

Pentatomoidea

Cydnidae

Sehirinae

Previous description : Leston, 1956*a*.

Species examined : *Sehirus luctuosus* Muls. and Rey (figs. 1–3), *S. bicolor* (L.), *S. dubius* (Scop.), *S. biguttatus* (L.), *Geotomus punctulatus* (Costa).

Female genitalia having an almost directly posterior aspect ; sternum VII complete, not cleft and not obscuring terminalia ; paratergites VIII continuous above anus and free from first gonocoxae ventrally ; paratergites IX, broad, flattened and almost meeting in mid-line beneath anus ; first gonocoxa large, rounded and with antero-dorsal corner produced as an apodeme ; first gonapophyses small, flap-like and membranously united ; sclerotized first and second rami distinct and curved ; anterior strut of gonangulum long and slender ; second gonocoxae slender and curved round posteriorly to meet in mid-line beneath paratergites IX, where they are enlarged and produced dorsally ; second gonocoxae joined to paratergite IX along whole of ventral edge of latter ; second gonapophyses membranous and flap-like and partially fused to membrane between second gonocoxae —the inter-gonocoxal membrane ; gonoplacs absent ; genital chamber large and sacciform, with a dorsal pouch posteriorly within precincts of segment VIII ; pair of ring sclerites present in posterior wall of dorsal pouch ; median spermatheca present with duct opening into dorsal pouch ; area of attachment of posterior dilator muscle of genital chamber often sclerotized.

The musculature of *S. luctuosus* and *S. bicolor* has been examined and the latter figured (fig. 98).

Cydninae

Species examined : *Cydnus aterrima* Forst.

Similar to structure in Sehirinae, but with paratergites VIII contiguous posteriorly ; gonapophyses larger and more sclerotized ; second gonapophyses united dorsally by membrane ; ring sclerites and gonoplacs absent.

Coriomelaeinae

Previous description : McAtee and Malloch, 1933.

Species examined : *Thyreocoris scarabaeoidea* (L.), *Coriomelana pulicarius* (Germ.), *Galgupha atra* A. & S. (fig. 5).

(a) *Thyreocoris scarabaeoides :* female genitalia similar to those of Sehirinae, but with gonapophyses heavily sclerotized and appearing as curved rods connected by membrane ; rami well developed and paratergites VIII fused in mid-line posteriorly.

(b) *Coriomelana pulicarius* and *Galgupha atra :* similar to Se hirinae in general shape, in fusion of paratergites VIII, *etc.*, but lacking rami and anterior strut of gonangulum ; second gonapophyses unrecognisable as such ; paired elongate sacs attached to base of second gonocoxae, the surface of the former being covered with minute projections ; ring sclerites and gonoplacs absent.

The Sehirinae and Cydnidae are very similar, with plate-shape type of female genitalia and with sclerotized rami. Those of *Thyreocoris* are also similar, but characteristically more sclerotized. The female genitalia in the other Coriomelaeinae are very different. Apart from *Thyreocoris*, the female genitalia in the latter subfamily are very specialised and indicate a homogeneous group. This may indicate that *Thyreocoris* is placed in the wrong subfamily, but, alternatively, it may be that *Thyreocoris* represents a remnant of the early Coriomelaeinae stock, isolated in the Palaearctic from the rest of the subfamily, which are mostly tropical.

Urostylidae

Previous descriptions: Yang, 1938*a*, 1938*b*, 1939.
Species examined: *Urolabida tenera* Hope.

First gonocoxae enlarged and obscuring rest of terminalia from external view; paratergites VIII large, apically rounded and not contiguous posteriorly; first and second rami present and interlocking; first gonapophyses rather large, flap-like and membranously united ventrally; gonapophyses and connecting membrane, posteriorly bordered by a fringe of long, dense hairs; first gonapophyses apically free from first gonocoxae; anterior strut of gonangulum slender; second gonapophyses partially sclerotized, rather flap-like and membranously joined to each other, except at extreme apex; second gonapophyses joined to inter-gonocoxal membrane; second gonocoxae continuous beneath anus, the fused part being separate from the part of the gonocoxa attached to the second ramus; an area of sclerotization attached to junction of second gonocoxa and second gonapophysis, carries the ring sclerite and supports the genital chamber; U-shaped sclerite present around opening of spermatheca into genital chamber; gonoplacs absent.

Brachyplatidae

Species examined: *Libyaspis* sp.

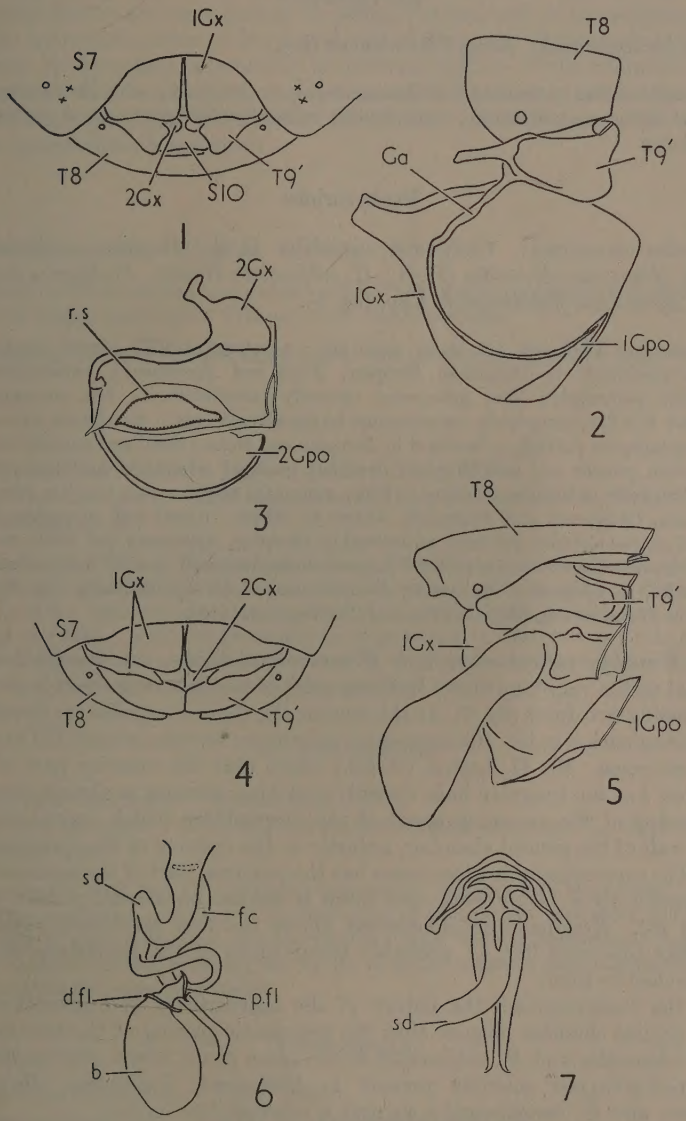
General shape and structure similar to Sehirinae; paratergites not contiguous posteriorly; paratergites VIII ventrally in contact with first gonocoxae; anterior apodeme of first gonocoxa short; first gonapophyses large and rami absent; anterior strut of gonangulum broad and well sclerotized; second gonocoxae joined in mid-line, but still possessing well developed apodemes; a flat sclerotization attached to anterior of second gonocoxae is presumably the second gonapophyses; two ring sclerites present; wall of genital chamber without sclerotizations; gonoplacs absent.

Scutelleridae

Scutellerinae

Species examined: *Anoplogonius nigricollis* Sign.

Paratergites VIII and IX about same size; first gonocoxa large with antero-dorsal apodeme very large and antero-ventral part rather membranous and produced anteriorly; sclerotized rami present and interlocking; anterior strut of gonangulum complete and slender; first and second gonapophyses large and flap-like and membranous; first pair united; second gonapophyses attached to inter-gonocoxal membrane; second gonocoxae fused posteriorly, not fusing with paratergite IX, but freely pivoting on posterior strut of gonangulum; genital chamber without ring sclerites, but with complicated sclerites around opening of spermathecal duct; gonoplacs absent.



FIGS. 1–7.—(1)–(3) *Sehirus luctuosus* Muls. and Rey (Cydnidae): (1) ventral view of female terminalia; (2) inner view of first gonocoxa and associated parts; (3) inner view of second gonocoxa and associated parts. (4) *Agonosoma flavolineatum* Lap. (Scutelleridae); ventral view of female terminalia; (5) *Galgupha atra* A. and S. (Cydnidae): inner view of right half of female genitalia; (6) *Hotea subfasciata* (Westw.) (Scutelleridae): spermatheca; (7) *H. curculionoides* (H.-S.): anchor-shaped sclerite surrounding opening of spermathecal duct.

Eurygastrinae

Species examined: *Eurygaster maurus* (L.).

Genitalia similar to those of Scutellerinae, but less sclerotized; with paratergites very large and contiguous posteriorly; rami partially reduced and anterior strut of gonangulum membranous.

Pachycorinae

Species examined: *Chelysoma variabilis* H.-S., *Deroplax redtenbacheri* (Mayr), *Hotea curculionoides* (H.-S.), *H. subfasciata* Westw., *Pachycoris torridus* Scop., *Agonosoma flavolineatum* Lap. (fig. 4).

Paratergites VIII and IX about same size; paratergites VIII almost meeting in mid-line posteriorly in *Chelysoma*, *Deroplax*, *Hotea* and *Agonosoma*; paratergites IX contiguous posteriorly; first gonocoxae ventrally nonsclerotized; first gonapophyses small and flap-like, completely membranous in *Agonosoma* only; membrane connecting first gonapophyses partially sclerotized in *Deroplax* and *Hotea*; rami and anterior strut of gonangulum present and sclerotized in *Deroplax*, partially sclerotized in *Hotea curculionoides*, but more or less membranous in rest; gonoplacs absent; ring sclerites present in *Agonosoma*, *Chelysoma*, and *Pachycoris*, absent in others; dorsal wall of postero-dorsal pouch of genital chamber partially sclerotized in *Deroplax*, *Agonosoma* and *Hotea curculionoides*; anchor-shaped sclerite situated in genital chamber wall, around entry of spermathecal duct, in *Chelysoma*, *Pachycoris*, *Deroplax* and *Hotea curculionoides* (fig. 7); also present in *Tectocoris diophthalmus* (Thunb.) (Pendergrast, 1957).

In *Deroplax redtenbacheri* and *Hotea curculionoides* the spermatheca is identical with a very long duct. In *Hotea subfasciata* the spermatheca is peculiar in possessing two ducts (fig. 6). In this species also there is a special sac developed as an invagination in the intersegmental membrane between sterna VII and the first gonocoxae. Mr. D. Leston (*in litt.*) states that the anterior part of this sac often has an irregular hole dorsally and this opening is almost opposite the opening of the accessory canal of the spermatheca which opens into the dorsal wall of the genital chamber, anterior to the opening of the spermathecal duct. The spermatheca in *Agonosoma* has the proximal part of the spermathecal duct similar to *H. subfasciata*, but there is neither an accessory duct nor a ventral sac. Externally in *Agonosoma* above the first gonocoxae there are finger-like processes (fig. 4), probably subdivisions of the gonocoxae as they are attached to them.

In the Pachycorinae, the nature of the spermatheca and sclerotizations of the genital chamber suggest that the systematic placing of the two species *H. curculionoides* and *H. subfasciata* in the same genus needs reinvestigation. The anchor-shaped sclerites present in *Chelysoma*, *Pachycoris*, *Deroplax*, *Tectocoris* and *H. curculionoides* suggest a monophyletic group.

Leston states that the special sac in *H. subfasciata* and the associated accessory duct to the spermatheca suggest that copulation may be abnormal in this species. The irregular hole sometimes present in the sac may be caused by the aedeagus being inserted into this sac, penetrating the dorsal wall and wall of the genital chamber; Leston (1952) has commented on the uniqueness of the aedeagus in this species. Sperm then liberated into the genital chamber

could migrate up the accessory canal into the spermatheca. The aperture of the accessory duct is not wide enough to permit the insertion of the aedeagus.

The sclerotized nature of the dorsal wall of the pouch of the genital chamber in many Pachycorinae is probably to prevent rupture of the chamber during copulation. The conjunctival appendages of the aedeagus press against the wall during copulation. The function of the other sclerotizations at the opening of the spermatheca is unknown.

Canopidae

Species examined : *Canopus impressus* (F.).

Similar to Schirinae with rami distinct and well sclerotized ; gonocoxae and paratergites of similar shape ; paratergites VIII not continuous posteriorly.

A special feature of the Canopidae is the possession of rectal sacs.

Tessarotomidae

Previous descriptions : Leston, 1953*a* ; Yang, 1935.

Species examined : *Eusthenes robustus* Lap., *Phloea corticata* Drury, *Piezosternum calidum* F.

Paratergites VIII and IX about same size in *Piezosternum*, paratergites IX the larger in *Eusthenes* ; paratergites VIII the larger in *Phloea* and partially fused to sternum VII which is cleft ; rami sclerotized and interlocking ; gonapophyses flap-like, but not membranous in *Phloea* ; rami and gonapophyses membranous in *Piezosternum* ; ring sclerites present in *Piezosternum* ; second gonocoxae rather membranous and more or less inseparable from inter-gonocoxal membrane in *Phloea* ; gonoplacs absent.

Acanthosomidae

Previous description : Rosenkranz, 1939.

Species examined : *Acanthosoma haemorrhoidale* (L.) (fig. 8), *Elasmostethus interstinctus* (L.).

Paratergites VIII and IX contiguous posteriorly ; former larger than latter ; second gonocoxae contiguous posteriorly ; anterior strut of gonangulum very short and broad ; both pairs of rami sclerotized and interlocking ; rami bearing membranous flaps—flap on first ramus of one side being opposed by flap on second ramus of same side, thus forming an incomplete sac ; gonoplacs absent.

Dinidoridae

Previous description : Yang, 1940.

Species examined : *Coridius* (= *Aspongopus*) *janus* (F.).

Paratergites IX larger than paratergites VIII and contiguous posteriorly ; broad sclerotized rami present and gonapophyses partially sclerotized ; second gonocoxae continuous posteriorly ; anterior strut of gonangulum weakly sclerotized ; cup-shaped sclerotization present in wall of genital chamber near opening of spermathecal duct ; gonoplacs absent.

Eumenotidae

Previous description: Esaki, 1930.
Species examined: *Eumenotes obscura* Westw.

Paratergites as in Dinidoridae; general shape of female genitalia like those in *Megymenum*; rami and gonapophyses partially sclerotized; second gonocoxae apparently completely membranous, rami thus not firmly fused to a dorsal sclerite; first ramus free from short and broad anterior strut of gonangulum; ring sclerites and gonoplacs absent; genital chamber without sclerotizations.

Pentatomidae

Previous descriptions[1]: Bonnemaison, 1952; Trukhanov, 1947; Jeannel, 1920; Vodjdani, 1954; Leston, 1955*a*, 1956*b*; Lacaze-Duthiers, 1853; Santoro, 1954; Dupuis, 1951; Puchkova, 1958.
Species examined: *Acoloba lanceolatum* (F.), *Palomena prasina* (L.), *Pentatoma rufipes* (L.), *Picromerus bidens* (L.), *Podops inuncta* (F.), *Stollia fabricii* Kirk.

Paratergites VIII continuous above anus in *Podops*, *Acoloba*, *Picromerus* and *Stollia*; rami and anterior strut of gonangulum membranous or absent; gonapophyses membranous in most cases; first gonapophyses often rather large and joined together by a large triangular shaped membrane—the triangulum of Verhoeff (1893); antero-ventral corner of first gonocoxa produced forwards; retractor muscle of first gonapophysis and retractor muscle of second gonapophysis absent; goblet-like sclerotized structures often attached to wall of genital chamber; gonoplacs absent.

The female genitalia of the Pentatomidae are very constant and are always without sclerotized rami. The first gonapophyses are joined by the triangulum and both retractor muscles of the gonapophyses are absent, this being associated with the loss of the anterior strut of the gonangulum and the rami. Pendergrast (1957) has shown that the spermatheca of this family is constant and characteristic and I have confirmed this.

Leston (1956*b*) has described an exserted ovipositor in this family, in *Birketsmithia*; he states that the exserted valves are not homologous with the exserted valves of the Lygaeid-type of ovipositor, but are modified gonocoxae.

The female genitalia of this superfamily may be considered as the plate-shaped type (*see* Dupuis, 1955), with a directly posterior or postero-ventral aspect; members of this group usually oviposit on the surface of leaves, trunks, *etc.* The paratergites are very large and together with the first gonocoxae are the most conspicuous parts of the terminalia. The gonapophyses are small and usually membranous and flap-like. In most families the rami are sclerotized, gently curved and interlocking. Ring sclerites may be present. The first gonocoxa is not fused to paratergite VIII and gonoplacs are absent. Paratergites VIII and IX and the second gonocoxae meet in the mid-line posteriorly. Paratergites VIII, when fusing, form a broad sclerite dorsal to the anus. The second gonocoxae, when fusing, form a narrow bridge-like sclerite immediately

[1] Additional references to this and other families may be found in the following paper, received since the completion of this manuscript:

Štys, P., 1958, A guide to the literature on the female ectodermal genitalia of Heteroptera. *Acta Musei Reginaehradecensis S.A.L.* **1958**: 45–64.

beneath the anus and sternum X ; even when not fusing, they appear as a bridge-like sclerite and characterise the genitalia of the Pentatomoidea.

There is a tendency for the development of additional sclerotizations in the wall of the genital chamber, especially around the opening of the spermathecal duct and at the attachment of the posterior dilator muscle of the genital chamber. Other special structures associated with the transmission of symbionts may be present.

The musculature in the group is rather constant and characteristically all species seem to be without the retractor muscle of the first gonapophyses. In species without sclerotized rami, the retractor muscle of the second gonapophysis is also absent (fig. 99).

There is nothing in the morphology of the female genitalia to support or disprove the division of the superfamily into two groups, as suggested by Leston (1956*c*, 1958). Several families by the presence of ring sclerites and/or the retention of sclerotized and interlocking rami, can probably be regarded as the least specialised. The female genitalia of the Pentatomidae, by their reduced nature, suggest that this family is the most highly evolved in the taxon. This is supported by the constant and specialised structure of the spermatheca (Pendergrast, 1957).

Leston (1955*a*, 1956*a*, 1956*b*) has misinterpreted the second gonocoxa in his accounts of the female genitalia of the Pentatomoidea, but applies a consistent nomenclature in the group. What he calls the second gonocoxa (= second valvifer) is paratergite IX. His " ventral sclerites of segment 9 " (Leston, 1956*a*) are the fused second gonocoxae, as is the median bridge-like piece he figures (Leston, 1955*a*) in *Piezodorus lituratus* (F.) beneath sternum X.

There is general agreement that this is a natural group, but at the family and subfamily level, however, this is not so. The families recognised in this study follow Leston (*unpublished*). Only in the Pentatomidae do the female genitalia provide a set of useful delimiting characters.

Pyrrhocoroidea

Pyrrhocoridae

Previous descriptions : Gupta, 1951 ; Ludwig, 1926 ; Mayer, 1875 ; Seidel, 1924 ; Pruthi, 1924.

Species examined : *Dysdercus cingulatus* (F.), *D. fasciatus* Sign. (figs. 28, 29), *Pyrrhocoris apterus* (L.).

Paratergites VIII small, triangular, well separated from each other and not fused to first gonocoxae ; paratergites IX large, almost contiguous posteriorly ; first gonocoxae rather rounded in outline with an antero-dorsal apodeme ; first gonapophyses membranous and flap-like and ventrally united by membrane ; rami short, sclerotized, slightly curved and interlocking ; anterior strut of gonangulum slender ; second gonocoxae broad and flattened, curved round posteriorly, apically turned ventrally and fusing in mid-line, forming an M-shaped structure ; second gonocoxae partially fused to paratergites IX along ventral edge of latter ; second gonapophyses membranous, flap-like and partially fused to inter-gonocoxal membrane ; gonoplacs absent ; median spermatheca present ; genital chamber large and with a dorso-posterior pouch.

The musculature of *D. fasciatus* has been investigated and is shown in figure 100. All muscles appear to be present.

The female genitalia of this superfamily are of the plate-shaped type and rather similar to those of the Pentatomoidea. There is a median spermatheca, but gonoplacs are absent. The shape and complete fusion of the second gonocoxae, together with the presence of the retractor muscle of the first gonapophysis, precludes the inclusion of the Pyrrhocoridae in the Pentatomoidea. Since they have not the laciniate type of ovipositor, the Pyrrhocoroidea cannot be included in the Lygaeoid-Coreoid complex; the ovipositor is not of the true laciniate type as stated by Leston (1955*b*). All three pairs of ovipositor valves are not present as stated by Gupta (1951), who calls the gonocoxae the basivalvulae, and the gonangulum the valvifer.

Since the ovipositor of the Largidae is unlike that of the Pyrrhocoridae, but like that of the Lygaeidae, family status for the Largidae, first proposed by China (1954), has been accepted and the family treated in the Lygaeoidea, thus leaving the Pyrrhocoridae as the only family in the superfamily. The present work supports Southwood (1956*a*) in the erection of a superfamily. Southwood also included Largidae, but stated that more information was required on this family before its taxonomic position could be fully ascertained.

Coreoidea

Coreidae

Previous descriptions: Brown, 1955; Snodgrass, 1933; Tower, 1913.

Species examined: *Coreus marginatus* (L.) (figs. 9, 10), *Leptoglossus occidentalis* Heid.

Sternum VII cleft, but not to base; paratergites IX rather large and rounded and almost contiguous posteriorly; paratergites VIII triangular, small and separate from first gonocoxae; first gonocoxae large and rounded with anterior apodeme in middle of anterior edge; first gonapophyses rather elongate and sclerotized and with short, obliquely angled, sclerotized rami; anterior strut of gonangulum short, flattened and with a distinctly projecting apodeme anteriorly; second gonocoxae broad, rather flat and freely pivoting on ventral end of posterior strut of gonangulum, which is fused to paratergite IX; second ramus sclerotized and interlocking with first; second gonapophysis slender proximally, but apically expanded where it forms an incomplete cylindrical structure and in *Coreus* is joined to its opposite number; small sclerites at base of and attached to second gonocoxae; ring sclerites present; gonoplacs absent; median functional spermatheca present; a small spherical sac attaches to membrane between first gonapophysis and first gonocoxa in *Coreus*.

Colobathristidae

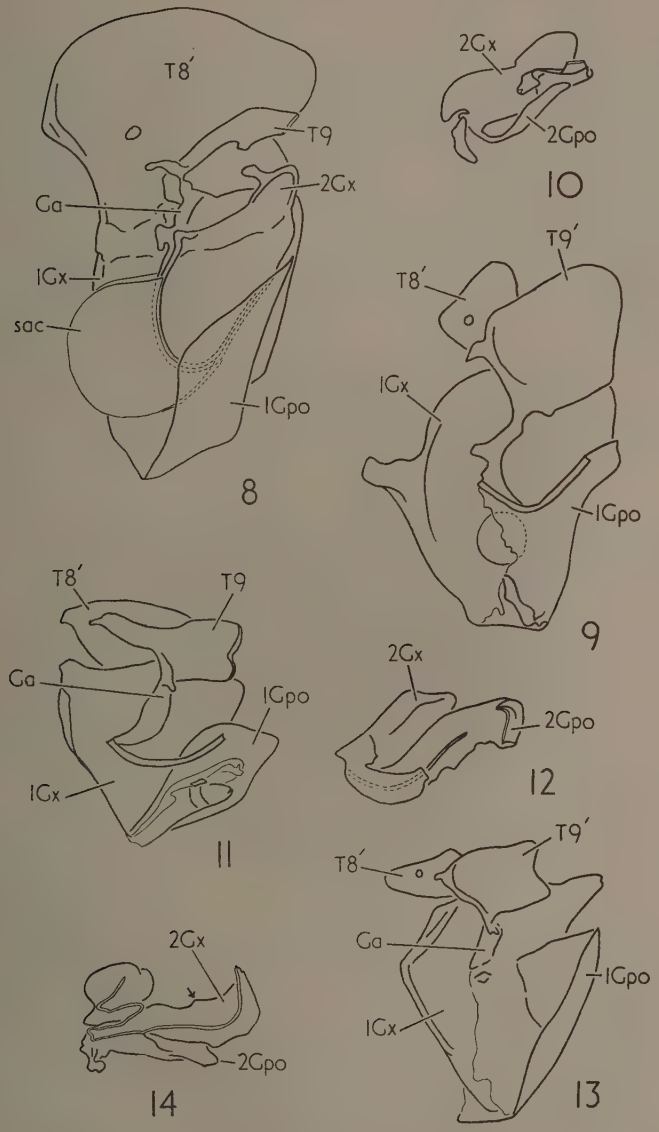
Species examined: *Phaenacantha* sp. (figs. 19, 20).

Very similar to general structure in *Coreus*; first gonocoxa without distinct anterior projecting apodeme; first gonapophyses short antero-posteriorly, but broad dorso-ventrally; rami sclerotized, but rather short; second gonocoxa and gonapophysis as in *Coreus*, but both structures joined to their opposite number; gonoplacs absent; without sclerotized expansions supporting genital chamber.

Rhopalidae

Previous description: Woolley, 1949.

Species examined: *Myrmus miriformis* (Fall.), *Rhopalus subrufus* (Gmel.)



Figs. 8–14.—(8) *Acanthosoma haemorrhoidale* (L.) (Acanthosomidae) : inner view of right half of female genitalia ; (9)–(10) *Coreus marginatus* (L.) (Coreidae) : (9) first (10) second gonocoxa and associated parts ; (11)–(12) *Rhopalus subrufus* (Gmel.) (Rhopalidae) : (11) first (12) second gonocoxa and associated parts ; (13)–(14) *Alydus calcaratus* (L.) (Alydidae) : (13) first (14) second gonocoxa and associated parts.

(figs. 11, 12), *Stictopleurus crassicornis* (L.), *Harmostes reflexulus* (Say), *Leptocoris trivittatus* (Say).

Genitalia usually withdrawn well into and obscured by sternum VII, which is not cleft; apodeme at dorsal angle of gonangulum very large and produced anteriorly; rami sclerotized, obliquely angled and interlocking; first rather rounded, but sclerotized and joined ventrally by membrane, variously folded and carrying characteristically a U-shaped sclerite; second gonocoxae rather short, broad, sclerotized and not meeting in mid-line posteriorly; second gonapophyses broad, sclerotized, carrying rami on outer face and joined apically and to second gonocoxae dorsally; gonoplacs absent; median spermatheca present; wide sclerotized expansions present at base of second gonocoxae.

The musculature of *Rhopalus subrufus* and of *Myrmus miriformis* has been examined. The retractor muscle of the first gonapophysis is present and the posterior dilator muscle of the genital chamber appears to have split into two.

In *Stictopleurus* and *Harmostes* the genitalia, instead of being rather flattened as in *Rhopalus* and *Myrmus*, are rather elongate dorso-ventrally. The terminal view of the abdomen (posterior margin of segment VII) is triangular in *Stictopleurus* and *Harmostes* and semicircular in the other genera mentioned. This accounts for the difference in shape of the female genitalia.

Alydidae

Species examined: *Alydus calcaratus* (L.) (figs. 13, 14), *A. pluto* Uhler, *Megalotomus 5-spinosus* (Say), *Tollius curtulus* (Stål).

Paratergite VIII small, triangular and free from first gonocoxa; paratergite IX large and quadrate; first gonocoxa produced posteriorly; first gonapophysis with exposed part sclerotized, but rest of this elongate structure only partially so; first ramus absent; anterior strut of gonangulum represented by a faint trace of sclerotization; second gonocoxae broad, sclerotized, boat-shaped and fused posteriorly; second gonapophyses sclerotized, shorter than and fused to second gonocoxae; second ramus and gonoplacs absent; sclerotized expansions at base of second gonocoxae fusing in mid-line to form a complete and complicated support to genital chamber; median spermatheca present.

The genitalia in the Coreoidea have usually a posterior aspect and are of the plate-shaped type in *Rhopalus* and *Myrmus*, but other genera studied appear somewhat closer to the laciniate type. The first gonocoxa is not fused to paratergite VIII and gonoplacs are absent. The second gonocoxae, if fusing in the mid-line posteriorly, do not form a median narrow bridge-like sclerite as in the Pentatomoidea, nor an M-shaped sclerite as in the Pyrrhocoroidea. Sclerotized and interlocking rami are usually present, except in the Alydidae. Ring sclerites may be present.

The retractor muscle of the first gonapophysis is present, at least in species with sclerotized rami and anterior strut of the gonangulum present. This is not the case in Pentatomoidea. There is a tendency for the development of sclerotized expansions at the base of the second gonocoxae; these support the genital chamber and are most complicated in the Alydidae.

The study of the female genitalia supports the conclusion of Reuter (1912) that the Rhopalidae and the Alydidae should be of family rank. The Coreidae are the more primitive in retaining ring sclerites, in having the second gonocoxae free from each other and in having elongate gonapophyses and only small

sclerotizations supporting the genital chamber. The Alydidae appear to be the most specialised as they have lost the rami, have the second gonocoxae fused with each other and with the second gonapophyses and have very complicated sclerotized expansions supporting the genital chamber. The Rhopalidae, by possessing the U-shaped sclerite between the first gonapophyses, are very distinct. This family also has the posterior dilator muscle of the genital chamber divided into two, but this may also be so in the other families of the Coreoidea. Southwood (1956*a*) finds, on egg structure, the Rhopalidae to be more specialised than the Alydidae.

If the two superfamilies, Lygaeoidea and Coreoidea, are kept separate, the Colobathristidae appear more correctly placed in the latter on the character of the female genitalia. Pendergrast (1957) was unable to associate the Colobathristidae with other families on the characters of the spermatheca. Southwood (1956*a*) states that the egg is quite different from that in the Lygaeidae.

Lygaeoidea

Lygaeidae

Previous descriptions : Bonhag and Wick, 1953 ; Ekblom, 1926 ; Ludwig, 1926; Scudder, 1957*g*.

Species examined : this family has been investigated more completely than any other in order to examine the structural stability of the female genitalia within a single family. In all about 320 species, comprising 247 genera have been examined. *Gastrodes grossipes* (Deg.) (Rhyparochrominae) is figured (figs. 21, 22).

Sternum VII usually cleft to base ; paratergite VIII triangular and separate from first gonocoxa ; all parts of ovipositor complex, usually sclerotized (save gonapophyses in Lygaeinae) ; first gonocoxa more or less triangular in shape, to which elongate, laciniate first gonapophyses attach ventrally ; first and second rami long, rod-like, acutely angled and interlocking ; first and second gonapophyses usually united longitudinally, the former almost always in basal two-thirds only ; anterior strut of gonangulum rather broad and flattened ; second gonocoxa crescentic in shape, slightly flattened, free posteriorly and articulating with ventral end of posterior strut of gonangulum at its mid-point ; second gonapophyses sclerotized and laciniate ; median spermatheca present ; ring sclerites often present ; sclerotizations in wall of genital chamber otherwise usually absent ; gonoplacs absent.

The musculature of *Oncopeltus fasciatus* (Dall.), *Ischnodemus sabuleti* (Fall.), *Scolopostethus thomsoni* Reut. and *Gastrodes grossipes* has been examined and found to be the same as that in *Dicranocephalus* (Scudder, 1957*a*).

Within the Lygaeidae the structure of the female genitalia is remarkably constant, differing in very few genera. In the Pachygronthinae, Oxycareninae and Heterogastrinae (in part) and to a lesser extent in the Cyminae, the first gonocoxae are conspicuously elongate dorso-ventrally and appear to extend half way along the abdomen ventrally. The Oxycareninae are distinct in having the abdomen conspicuously truncate posteriorly.

In *Harmostica ornata* (Dist.) (Rhyparochrominae : Stygnocorini) the female genitalia are atypical and the ovipositor is not long and laciniate. Instead it is short and the second gonapophyses are very broad.

In *Bubaces castaneus* Dist. (Rhyparochrominae : Lethaeini) there is an additional hook-like sclerotized projection to the inside of the second gonocoxae.

The female genitalia of the Lygaeinae are distinct. There is a reduction of the sclerotization of the gonapophyses with the formation of isolated sclerites and broadening and folding of the membranous parts of the gonapophyses. This is adequately illustrated by Bonhag and Wick (1953).

In Malcinae a short laciniate ovipositor is present. The anterior strut of the gonangulum is parallel to the gonapophyses and paratergite IX therefore appears more posterior than usual. The second gonocoxa is a rather large quadrate structure and ring sclerites are present.

The female genitalia of this group are distinct in shape and structure, as described above. Although the elongation in the Pachygronthinae, Oxycareninae and Heterogastrinae may indicate a close affinity of these three subfamilies, supported by the position of dorsal abdominal gland openings and abdominal spiracles, the lack of such elongation in some genera (e.g. *Masoas* (Heterogastrinae)) introduces the need for caution in this grouping. The truncate terminalia in Oxycareninae characterises this group and isolates them from other subfamilies. The structure in Lygaeinae suggests that this subfamily should be placed apart from the rest. That the Lygaeinae are distinct has been shown by Nuorteva (1956) in their salivary gland structure, and Manna (1951) has pointed out that they are unique in their loss of the m-chromosomes, characteristic of all other Lygaeoidea (and Coreoidea). The Orsillinae have the typical Lygaeid type of genitalia and do not have the gonapophyses modified as in the Lygaeinae. I consider that the former should be moved from the Lygaeinae and placed as a separate subfamily. Ashlock (1957), from a study of the male genitalia, has also concluded that the Lygaeini and Orsillini are not at all closely related.

Pendergrast (1957), in stating that " The spermatheca of the Lygaeidae are extremely diverse and it has proved quite impossible to list spermathecal characters for the group ", and further, " there is a bewildering diversity in its form even amongst members of the same subfamily ", was in fact demonstrating the unworkable nature of the then accepted supra-generic grouping in Lygaeidae. The present study, by abandoning some of the traditional supra-generic divisions, shows, in fact, that the spermatheca can provide valuable taxonomic characters in this family.

I have examined representatives of the majority of the world genera of the Lygaeidae and have been able to establish the value of the spermatheca in most subfamilies. It is of use at different taxonomic levels in the different subfamilies. All members of the Oxycareninae examined have a similar type of spermatheca ; this may indicate that it provides a good subfamily character in this group. In the Heterogastrinae various generic types are found and in *Dinomachus* it is a good specific character (Scudder, 1957*c*). In the Orsillinae and Ischnorhynchinae, good generic characters are seen. Perhaps the most interesting use of the spermatheca has been in the tribal classification of the Rhyparochrominae (Scudder, 1957*d*). Here tribes suggested by the position of spiracles, trichobothria and in part by chromosome number, were clearly delimited on spermathecal structure, expecially in the Rhyparochromini. The independent work of Ashlock (1957) on the aedeagus in general also supports the classification based on the above characters. In the Rhyparochromini,

the spermatheca cannot satisfactorily be used below the tribal level, but in the other tribes of the Rhyparochrominae, good generic characters are evident.

Stenocephalidae

Previous description : Scudder, 1957*a*.

Species examined : *Dicranocephalus agilis* (Scop.), *D. albipes* (F.), *D. insularis* (Dallas), *D. lauticeps* (Stal), *D. lateralis* Sign., *D. marginatus* (Ferrari), *D. medius* (Muls. & Rey), *D. punctipes* (Stål), *D. testaceus* (Stål), *D. tunetanus* Horv., *D. pallidus* Sign., *Psotilnus mucronifer* Stål.

Identical in structure with the female genitalia of Lygaeidae.

Largidae

Species examined : *Largus cinctus* H.-S., *Lohita grandis* (Gray).

Identical in structure with Lygaeidae, but having the gonapophyses more sclerotised, especially the second pair.

The ovipositor is of the laciniate type and not the plate-shape type as stated by Southwood (1956*a*).

Berytinidae

Species examined : *Berytinus minor* (H.-S.), *B. clavipes* (F.), *Gampsocoris punctipes* (Germ.), *Metatropis rufescens* (H.-S.) (figs. 15, 16).

The female genitalia are almost identical in structure with those of the Lygaeid subfamily Malcinae, but have the second gonocoxae crescentic instead of quadrate in shape.

Piesmidae

Previous description : Wille, 1929 ; Drake and Davis, 1958.

Species examined : *Piesma maculata* (Castel.) (figs. 17, 18).

Sternum VII cleft to base ; paratergite IX and first gonocoxa about same size, with paratergite VIII smaller ; otherwise very similar to Lygaeidae, with gonapophyses shorter and broader, but nevertheless laciniate.

The female genitalia of the Lygaeoidea have a ventral aspect and the superfamily may be said to have a laciniate type of ovipositor, without gonoplacs and with paratergite VIII not fused to the first gonocoxa. A median spermatheca is present and ring sclerites may also occur.

The genitalia of most Lygaeidae, Largidae and Stenocephalidae are almost indistinguishable. The Malcinae (Lygaeidae) and Berytinidae seem to be related on the structure of the female terminalia. The Piesmidae are very similar to the Lygaeidae on the one hand and to the Berytinidae on the other ; they undoubtedly belong in the Lygaeoidea and not in the Tingoidea, as believed until comparatively recently. The general shape of the sclerites visible externally (paratergites VIII and IX and first gonocoxae) in the Berytinidae and Malcinae is very similar to that seen in families possessing the plate-shape type of ovipositor.

Manna (1951) pointed out that the Lygaeoidea and Coreoidea were unique in the Heteroptera in possessing a pair of m-chromosomes. The Lygaeoidea generally have a low chromosome number and an XY sex-determining mechanism, whilst the Coreoidea have a higher chromosome number and an XO sex-determining mechanism. These appear to be fairly reliable characters. The Stenocephalidae were placed close to the Lygaeidae (Scudder, 1957*a*) on morphological grounds and a recent investigation of the cytology of *Dicranocephalus agilis* (Scop.) (Lewis & Scudder, 1958) shows it to have a diploid chromosome number of 12A + X + Y, a Lygaeoid complement and sex-determining mechanism.

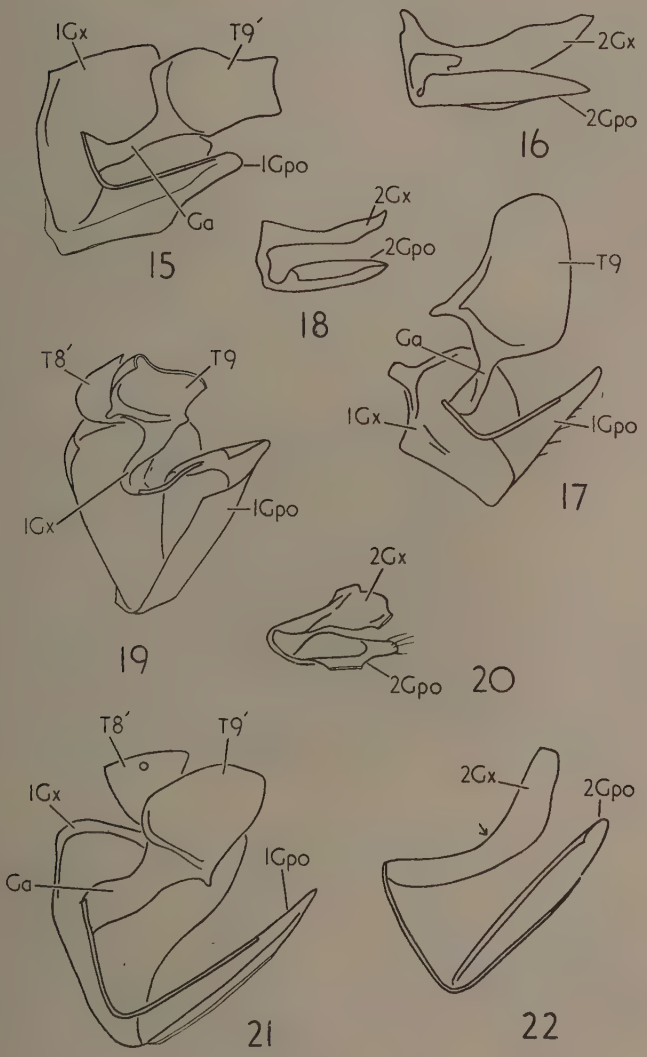
Pruthi (1925) stated that the male genitalia of the Lygaeidae can be distinguished by the total absence of conjunctival appendages. Ashlock (1957) states that conjunctival appendages in the Lygaeidae, if present, are in the form of relatively small inflatable lobes or, as in some Myodochina, in the form of spines borne on the conjunctiva or on inflatable lobes. The Lygaeidae (except the Heterogastrinae and Pachygronthinae) have the terminal part of the vesica, that part called by Ashlock " the gonoporal process of the vesica ", long, flagellum-like with the sclerotized ejaculatory duct within. No such vesica has yet been demonstrated in the Coreoidea. Elsewhere, I have shown (Scudder, 1957*a*) that the Stenocephalidae possess the long, flagellum-like vesica together with conjunctival appendages. The Coreoidea are characterised by having conjunctival appendages. Pruthi (1925) stated that the Berytinidae were without any distinct conjunctival appendages and have a flagellum-like vesica. He based his conclusions on *Berytinus minor* and *Hubertiella cardamoni*. I have erected and examined the aedeagus of *Berytinus minor*, *B. clavipes*, *Gampsocoris punctipes* and *Metatropis rufescens* and find that the conjunctiva has a pair of small, rounded and partially sclerotized lateral appendages, what Pruthi called " insignificant thick patches in the lateral region ". Also the vesica has long finger-like appendages and the gonoporal process of the vesica is flagellum-like.

The Largidae are said to be without conjunctival appendages and with a flagellum-like vesica (Pruthi, 1925), but *Lohita grandis* has two acicular conjunctival appendages. It thus appears that the Lygaeidae only; and not the Lygaeoidea as a whole, lack conjunctival appendages, and even in this family, conjunctival lobes and spines may be present.

From this it can be seen that the male genitalia of the Coreoidea and Lygaeoidea are not distinct. There is a gradual loss of conjunctival appendages as one passes successively through the families Stenocephalidae, Largidae, Berytinidae, Lygaeidae to the Piesmidae, where they are completely absent, except in *Miespa* (Drake and Davis (1958).)

Pendergrast (1957) has shown that the Coreoidea are characterised by the absence of a proximal spermathecal pump flange. In the Lygaeidae a proximal flange is usually present. In the Berytinidae it is absent or poorly developed, but in the Colobathristidae, Largidae and Stenocephalidae it is present.

The division between the Coreoidea and Lygaeoidea suggested by the nature of the principal salivary gland (Southwood, 1956*b*), does not coincide with the division obtained when other characters are considered. Whilst the Piesmidae and Lygaeidae (except Lygaeinae) have three lobes to the principal salivary



FIGS. 15–22.—(15)–(16) *Metatropis rufescens* (H.-S.) (Berytinidae): (15) first (16) second gonocoxa and associated parts; (17)–(18) *Piesma maculata* (Castel.) (Piesmidae): (17) first (18) second gonocoxa and associated parts; (19)–(20) *Phaenacantha* sp. (Colobathristidae): (19) first (20) second gonocoxa and associated parts; (21)–(22) *Gastrodes grossipes* (Deg.) (Lygaeidae): (21) first (22) second gonocoxa and associated parts.

gland, the Coreidae, Rhopalidae, Alydidae and Stenocephalidae have four. The number of lobes in the Largidae is not known.

As mentioned earlier, the female genitalia of the Colobathristidae are similar to those of the Coreidae, but have some affinities with the Lygaeidae. Pruthi (1925), however, regarded the male genitalia as showing that hardly more than subfamily status in the Lygaeidae was warranted for this group.

The position of the trichobothria on the abdomen, perhaps the best morphological character for distinguishing the Coreoidea from the Lygaeoidea, is probably only of minor importance and not sufficient to justify separate status if other characters so warrant a single superfamily. At present the Lygaeoidea are characterised by possessing the abdominal trichobothria on sterna V, VI and VII in the outer thirds of the sterna, whilst the Coreoidea have the corresponding organs in the median thirds. The antennal insertion character, often stated to separate the Lygaeoidea and Coreoidea, does not hold good; it breaks down in the Ninini (Lygaeidae, Cyminae) (Scudder, 1957*b*). The membranal venation in the Coreoidea is stated to consist of numerous and anastomosing veins, whilst the Lygaeoidea is said to possess only a few veins. It should be noted that the Stenocephalidae have a large number of anastomosing veins (Scudder, 1957*a*).

The above facts suggest that there may only be one superfamily involved, with the Coreidae and Lygaeidae or the Piesmidae as the two extremes.

Aradoidea

Dysodiidae

Species examined: *Dysodius crenulatus* Stål (figs. 23, 24).

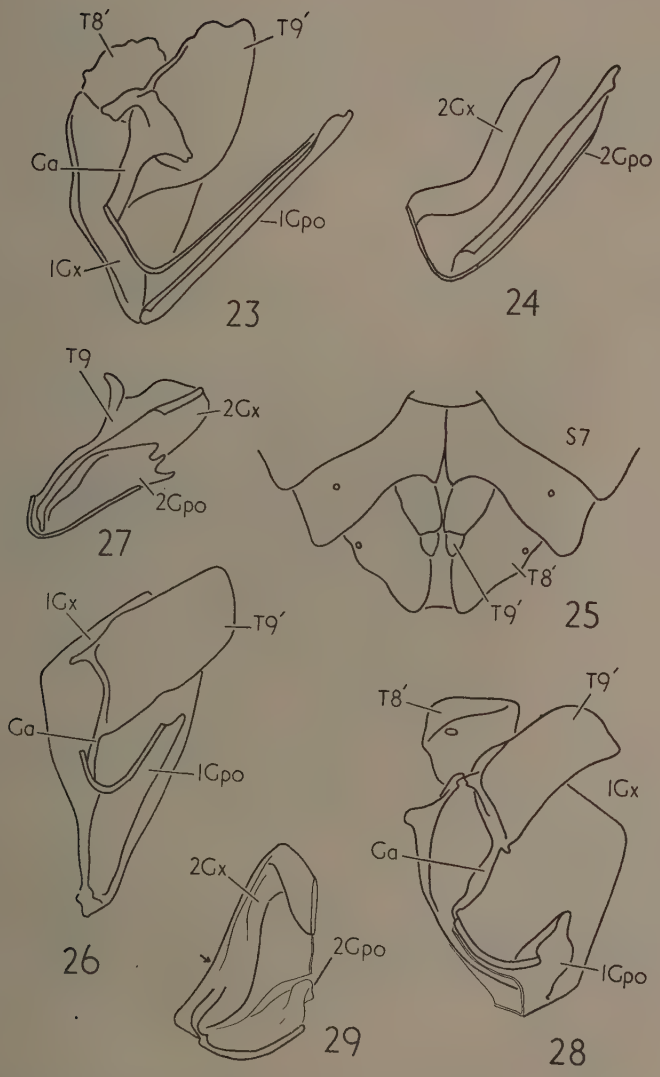
Sternum VII cleft almost to base; paratergite IX larger than paratergite VIII, first gonocoxa triangular in shape, closely associated with but not fused to paratergite VIII and bearing the laciniate and sclerotized first gonapophyses; rami long, sclerotized, acutely angled and interlocking; second gonocoxae crescentic in shape, free posteriorly and not particularly closely applied to paratergites IX; anterior strut of gonangulum slender; large apodeme conspicuous at dorsal corner of gonangulum; gonoplacs absent; median spermatheca present.

Aradidae

Previous descriptions: Leston, 1955*b*; Tamanini, 1950, 1955; Tropin, 1951.

Species examined: *Aradus cinnamomeus* (Panz.), *A. depressus* (F.) (figs. 25–27), *A. debilis* Uhl., *A. blaisdelli* van D.

Terminalia flattened; sternum VII partially cleft; paratergites VIII very large and projecting well beyond end of abdomen, and not fused with first gonocoxae; paratergites IX small, smaller than first gonocoxae; first gonapophyses elongate and sclerotized; anterior strut of gonangulum very slender; both pairs of rami sclerotized, rather obliquely angled and interlocking; second gonapophyses elongate, heavily sclerotized distally, with a dense covering of long, fine hairs and often apically bifid or trifid; second gonocoxae often joined dorsally in the mid-line posteriorly, partially sclerotized, rather elongate and closely associated with paratergites IX; gonoplacs absent; median spermatheca present; often M-shaped sclerite present at opening of spermathecal duct into genital chamber.



FIGS. 23–29.—(23)–(24) *Dysodius crenulatus* Stal (Dysodiidae): (23) first (24) second gonocoxa and associated parts; (25)–(27) *Aradus depressus* (F.) (Aradidae): (25) ventral view of female terminalia; (26) first (27) second gonocoxa and associated parts; (28)–(29) *Dysdercus fasciatus* Sign. (Pyrrhocoridae): (28) first (29) second gonocoxa and associated parts.

Dupuis (1955) states that the genitalia are of the plate-shaped type and Leston (1955*b*) states that the female genitalia of the Aradidae are of the same general type as in the Pentatomoidea and Coreoidea and he associated the Aradidae with these, especially with the latter. I find this relationship to be true in so far as the genitalia are flattened and externally resemble the plate-shaped type. Internally, however, the genitalia are closer to the laciniate type of ovipositor. The gonapophyses are sclerotized and the second pair are quite unlike the condition in the Coreoidea. Leston (1955*b*) has interpreted paratergite IX as the second gonocoxa. The sclerite he calls the " inter-valvifer sclerite " is the bridge connecting the dorsal part of the second gonocoxae.

Cimicoidea

Nabidae

Previous descriptions : Ekblom, 1926 ; Kullenberg, 1947.

Species examined : *Nabis ferus* (L.) (figs. 30, 31), *N. limbatus* Dahl., *N. major* Costa, *N. rugosus* (L.), *N. rufusculus* Reut., *Pagasa fusca* (Stein).

Paratergite VIII small, triangular and ventrally joined to first gonocoxa ; paratergite IX large and rounded ; first gonocoxa large and triangular with dorso-anterior corner produced as a short flat apodeme ; dorsally first gonocoxa fused with paratergite IX ; first gonapophysis elongate, laciniate and sclerotized, with minute serrations apically on dorsal edge ; first ramus sclerotized and on apical half of first gonapophysis runs on interior face, on basal half on dorsal edge ; anterior strut of gonangulum sclerotized, broad and flat ; second gonocoxa broad, flat and sclerotized with dorsal edge thickened ; second ramus sclerotized and interlocking with first ramus, thus running on ventral edge of basal half of second gonapophysis and on outer face of apical half ; second gonapophysis elongate and laciniate with coarse serrations on dorsal edge ; gonoplacs firmly attached to apex of second gonocoxae, short with dorsal and ventral edges turned inwards forming incomplete boat-shaped structures ; true median spermatheca absent ; pseudospermathecae absent ; genital chamber with pouched " seminal depository ".

The musculature in *N. limbatus* is shown in figure 102.

The female genitalia of this family are of the laciniate type, eggs being deposited in plant tissue. The first gonocoxa in the Nabidae is fused to paratergite IX, but paratergite VIII is not completely fused to the first gonocoxa. The true median spermatheca and pseudospermathecae are absent, the sperm receiving function being taken over by the pouch of the genital chamber termed the seminal depository.

Carayon (1952*a*, 1952*b*, 1952*c*, 1952*d*, 1954, 1955) has described various modifications of the genital chamber associated with the phenomenon of haemocoelic fecundation practised in some Nabidae belonging to the subfamily Prostemminae. These modifications are mostly the development of accessory pouches and tissues associated with the genital chamber and the transmission of sperm.

The presence of longitudinal intersegmental muscles in the abdomen is indicative of a generalised structure.

Velocipedidae

Species examined : *Scotomedes alienus* Dist.

The female genitalia of *Scotomedes* are almost identical with the structure in the Nabidae.

Miridae

Previous descriptions : Davis, 1955 ; Knight, 1941 ; Kullenberg, 1946, 1947 ; Lacaze-Duthiers, 1853 ; Slater, 1950 ; Southwood, 1953 ; Wagner, 1952 ; Stichel, 1955.

Species examined : *Calocoris norvegicus* (Gmel.) (figs. 32, 33), *C. fulvomaculatus* (Deg.), *Lygus rugulipennis* Popp., *Liocoris tripustulatus* (F.), *Stenodema laevigatum* (L.), *Leptopterna dolabrata* (L.), *Monalocoris filicis* (L.), *Dicyphus stachydis* Reut., *Orthotylus ochrotrichus* Fieb., *Plagiognathus arbustorum* (F.).

Sternum VII in mid-line often produced as a small flap-like subgenital plate ; paratergite VIII completely fused to first gonocoxa and individuality of sclerites completely lost ; paratergites IX large and rounded posteriorly ; first and second gonapophyses long, laciniate and sclerotized, occasionally with minute serrations ; second gonapophyses often with a bulbous base ; rami sclerotized and running along gonapophyses as in Nabidae ; anterior strut of gonangulum slender and sclerotized ; second gonocoxa long, broad and sclerotized, dorsal edge thickened and with two transverse thickened ridges, one at point of articulation with posterior strut of gonangulum, and other near base ; gonoplac small, curved with dorso-internal angle produced anteriorly as an apodeme ; genital chamber with various thickenings and sclerotizations including paired ring sclerites ; genital chamber with ventral pouched " seminal depository "; median spermathecal gland (accessory gland) present.

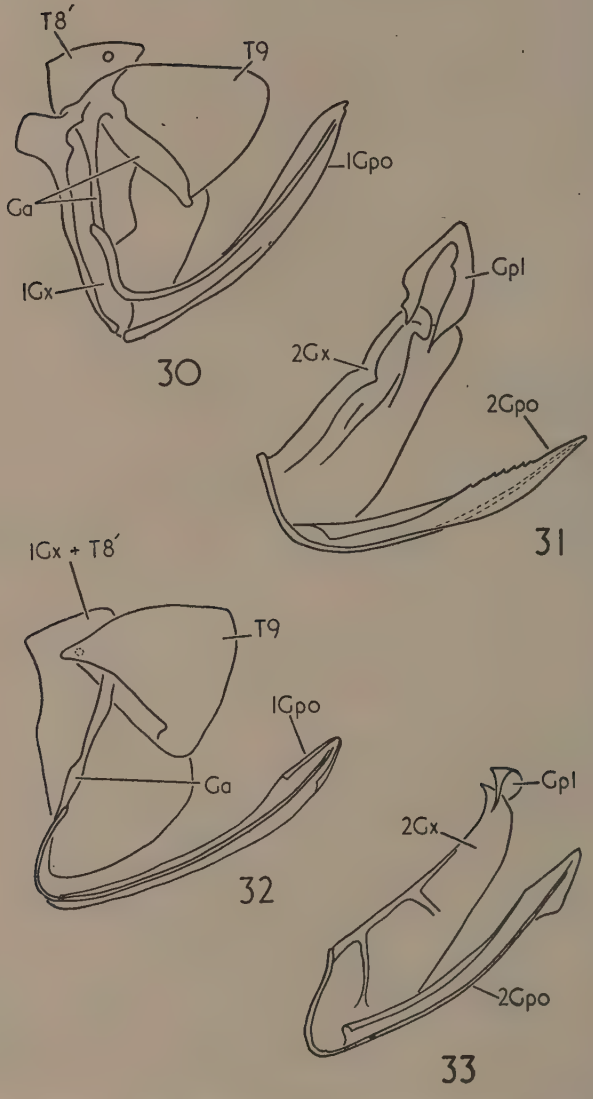
The musculature of *L. dolabrata* is shown in figure 103.

The female genitalia of the Miridae are similar to those of the Nabidae, but have the first gonocoxa and paratergite VIII completely fused, the first gonocoxa being free from paratergite IX. Also there is a median spermathecal gland and the second gonocoxa and genital chamber have different thickenings. The gonoplacs are also different.

As pointed out elsewhere (Scudder, 1956*b*), I do not agree with the interpretation of the first gonocoxa (= first valvifer) of Southwood (1953) and Davis (1955). The structure called the " eighth paratergum " by these authors, is the fused first gonocoxa and paratergite VIII. This interpretation is supported by the musculature.

The posterior strut of the gonangulum is called the " ramal plate " by Davis (1955). Davis considered the anterior strut of the gonangulum and the first ramus as one structure, an elongation of the processes from the base of the first gonapophyses, and did not agree with Kullenberg (1947) who thought that there were two parts involved. Kullenberg (1947) followed Snodgrass (1933) and considered that the ramus of the first gonapophysis extended anteriorly as the " fibula " and fused with an outgrowth of paratergite IX, the connecting piece or " verbindungstuck ". The thickened dorsal edge of the second gonocoxa, Davis (1955) called the valviferal apodeme. He further considered that the serrations of the gonapophyses probably reflected the oviposition habit of the various species. If this were true, species such as *Calocoris fulvomaculatus* ovipositing in woody tissue would be expected to have gonapophyses conspicuously more serrate than types ovipositing in softer tissue. Comparative studies suggest that this is not so.

The various thickenings and sclerotizations of the genital chamber have been described and illustrated by Davis (1955), and Slater (1950) has shown that these structures may be used as taxonomic characters and in demonstrating phylogenetic relationships. Slater and Davis (1952), Southwood (1953) and



Figs. 30–33.—(30)–(31) *Nabis ferus* (L.) (Nabidae): (30) first (31) second gonocoxa and associated parts; (32)–(33) *Calocoris norvegicus* (Gmel.) (Miridae): (32) first (33) second gonocoxa and associated parts.

Kelton (1955*a*, *b*, *c*) have given further instances of their value in this field so they will not be considered further.

The spermathecal gland is homologous with the true median spermatheca seen in such families as the Lygaeidae, Pentatomidae, *etc.* The seminal depository of the Miridae may be homologous with that in the Nabidae, but cannot be regarded as homologous with the sac-like pseudospermathecae in the Tingidae.

There is apparently little range of structure in the female genitalia in the Miridae, excluding the genital chamber. There is nothing to support or at variance with the system of classification of the Miridae by Carvalho (1956), Leston (1957), *etc.*

Isometopidae

Species examined : *Lindbergiola aureopilosa* Carv.

The female genitalia are almost identical with the structure in the Miridae, but the genital chamber is not as complicated and is apparently without a median spermathecal gland.

Anthocoridae

Previous descriptions : Carayon, 1952*e*, 1953*a*, 1953*b* ; China and Myers, 1929; Gomez-Menor Guerrero, 1956.

Species examined : *Anthocoris confusus* Reut., *A. gallarum-ulmi* (Deg.), *A. nemorum* (L.) (figs. 34–36), *Lyctocoris campestris* (F.).

Sternum VII very slightly produced posteriorly in mid-line ; paratergite VIII triangular and free from first gonocoxa ; paratergite IX rounded posteriorly, with a longitudinal split ventrally near second gonocoxa ; paratergite IX partially fused to first gonocoxa ; anterodorsal corner of first gonocoxa produced forwards as an apodeme ; first gonapophysis long, laciniate, sclerotized and with serrations on dorsal edge of apical half ; each first gonapophysis appears to be partially split longitudinally, the mesad parts being fused ; rami sclerotized, extending along edges of gonapophyses and interlocking ; anterior strut of gonangulum slender and sclerotized ; second gonocoxa elongate, broad and sclerotized, with dorsal margin thickened ; second gonapophysis long, laciniate and sclerotized, with both dorsal and ventral edge at extreme apex with minute serrations ; gonoplac small and sclerotized, with mesad projecting apodeme ; median spermatheca absent.

The female genitalia of the Anthocoridae are very similar to those of the Nabidae, differing especially in the split nature of the first gonapophyses and in rami running on the edges of the same.

An ovipositor is not always present in this family. China and Myers (1929) have shown that various stages in the reduction can be demonstrated in different species. In this family haemocoelic fecundation takes place (Carayon, 1953*a*, 1953*b*) and accessory structures may be developed (Carayon, 1952*e*).

Microphysidae

Species examined : *Loricula elegantula* (Baer.).

Almost identical with Anthocoridae, but with the gonapophyses elongate, parallel-sided with rounded apices and without serrations ; ring sclerites and gonoplacs present ; paratergite VIII fused to first gonocoxa ; median spermatheca absent.

Cimicidae

Previous descriptions : Abraham, 1934 ; Berlese, 1898 ; Carayon, 1953*c* ; Christophers & Cragg, 1922 ; Cragg, 1920 ; Davis, 1956 ; Hase, 1918 ; Heymons, 1899 ; Landois, 1869 ; Mather, 1952 ; Mellanby, 1939 ; Murray, 1914 ; Ribaga, 1897 ; Rothschild, 1912.

Species examined : *Cimex lectularius* L. (figs. 37, 38).

Paratergites VIII and IX and first gonocoxa rather quadrate in shape and about same size ; paratergite VIII not completely fused to first gonocoxa ; first gonocoxa partially fused to paratergite IX ; first gonapophysis short, broad and flat, but pointed and not rounded and flap-like ; first ramus partially sclerotized ; anterior strut of gonangulum absent ; second gonocoxa almost completely fused to paratergite IX ; second gonapophysis very reduced, rather flap-like ; second ramus hardly recognisable and not interlocking with first ; gonoplacs not recognisable as such ; median spermatheca absent ; Ribaga's organ present.

Davis (1956) has reviewed the literature and work on the Cimicidae and has done much original work. The female genitalia in this family are very reduced, but traces of the ovipositor, probably a laciniate one, are present, although China (1955*a*) states that such a structure is absent. Dupuis (1955) states that the Cimicidae have the plate-shape type of ovipositor. The occurrence of haemocoelic fecundation in this family suggests a close affinity with the Anthocoridae. The presence of a Ribaga's organ in the Cimicidae may be compared with a similar, perhaps homologous, structure present in some Anthocoridae (Carayon, 1952*e*).

Thaumastocoridae

Previous description : Drake and Slater, 1957.

Species examined : *Baclozygum depressum* Bergr.

Female genitalia very reduced ; paratergite VIII large and sclerotized ; small sclerotizations ventro-posteriorly probably represent reduced first gonocoxae ; paratergites IX not separate from tergum IX ; all other parts of genitalia derived from genital segments apparently absent ; median spermatheca absent ; genital chamber large and sac-like with two ventral sclerotized pouches.

This family has been placed next to the Lygaeidae ; it is quite unlike this family morphologically. The ventral sclerotized pouches to the genital chamber may be pseudospermathecae. The loss of parts of the genitalia and absence of a true median spermatheca, together with the absence of abdominal trichobothria, indicate that the Thaumastocoridae should be placed close to the Cimicidae. This is in agreement with the findings of Kormilev (1955*a*) and Drake and Slater (1957).

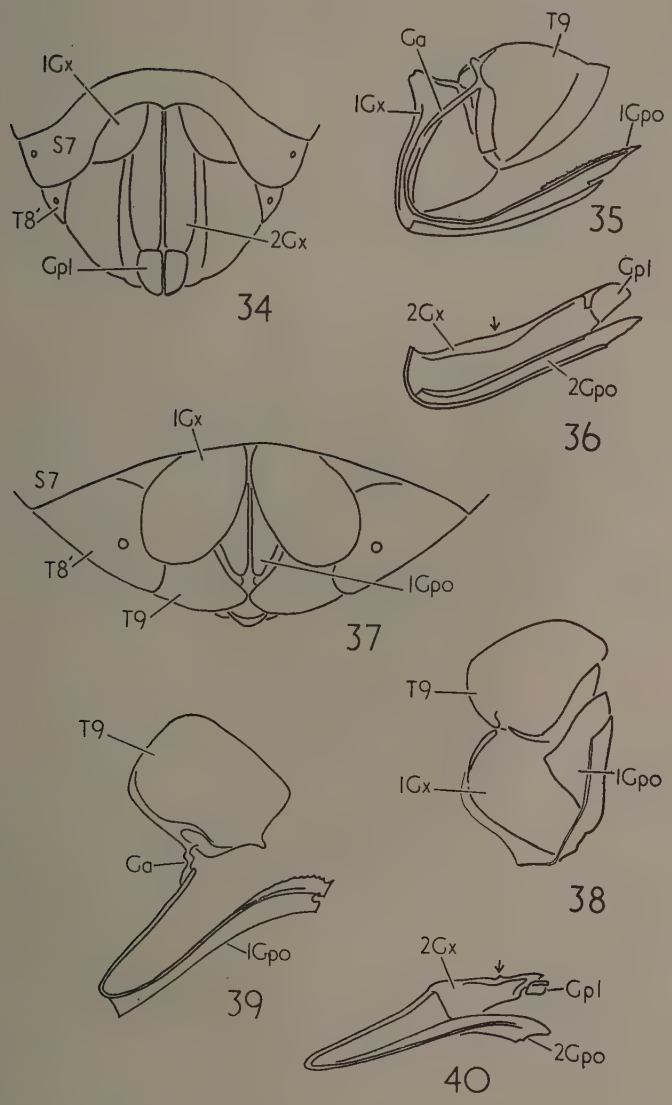
Polyctenidae

Previous descriptions : Ferris and Usinger, 1939 ; Hagan, 1931 ; Jordan, 1912.

Species examined : *Hesperoctenes* sp.

First gonocoxae, only, distinguishable in the species examined ; median spermatheca absent.

Hagan (1931) found that a spermatheca was absent in this family. Pseudospermathecae are also apparently absent. What may be regarded as the analogue



FIGS. 34–40.—(34)–(36) *Anthocoris nemorum* (L.) (Anthocoridae): (34) ventral view of female terminalia; (35) first (36) second gonocoxa and associated parts; (37)–(38) *Cimex lectularius* L. (Cimicidae): (37) ventral view of female terminalia; (38) first gonocoxa and associated parts; (39)–(40) *Ceratocombus coleoptratus* (Zett.) (Dipsocoridae): (39) first (40) second gonocoxa and associated parts.

of a Ribaga's organ has been demonstrated in one species (Ferris and Usinger, 1939). This family is probably closely related, therefore, to the Cimicidae.

The Cimicoidea have the genitalia visible ventrally and primitively have a laciniate type of ovipositor for oviposition in plant tissue (*e.g.* Nabidae, Miridae and some Anthocoridae). The ovipositor may be reduced in some families (Cimicidae, some Anthocoridae, Thaumastocoridae), this being associated with oviposition on the surface and not in tissue. The ecto-parasitic viviparous Polyctenidae have lost almost all trace of an ovipositor.

In types with a well developed ovipositor, gonoplacs are present and the first gonocoxa is more or less fused to paratergite VIII. Distinct sclerotized rami are also present. The sperm receiving and storage function of the median spermatheca has been lost and when the latter is present it serves as a secretory organ. Sperm is received and stored in other analogous accessory structures (pseudospermathecae). Haemocoelic fecundation occurs in several families (Nabidae, Anthocoridae, Cimicidae, Polyctenidae) with the modification and specialization of organs accordingly.

Carayon (1950*b*, *etc.*) and Pendergrast (1957) suggest that the Cimicoidea be redefined to include the Nabidae and Velocipedidae, together with the Cimicidae, Anthocoridae, Microphysidae, Miridae, Isometopidae and Polyctenidae. The present work strongly supports this grouping and also suggests the inclusion of the Thaumastocoridae, a family placed in this superfamily by Drake and Slater (1957).

The female genitalia of the Velocipedidae further support the opinion of Blöte (1945), followed by Leston, Pendergrast and Southwood (1954), that this is probably a subfamily of the Nabidae.

Dipsocoroidea

Dipsocoridae

Species examined : *Cryptostemma alienum* H.-S., *Ceratocombus coleoptratus* (Zett.).

Ceratocombus coleoptratus (figs. 39, 40) : sternum VII large and produced posteriorly to cover terminalia ; paratergite VIII incompletely separated from tergum VIII ; paratergite IX not separate from tergum IX ; first gonocoxa indistinct, probably represented by an area of sclerotization folded back on sternum VII internally ; first gonapophyses partially split and mesad portions membranously joined, otherwise elongate and sclerotized and tips with minute serrations on dorsal edge ; rami sclerotized and interlocking ; second gonapophyses elongate, sclerotized and united except at extreme apex ; second gonocoxa broad, flat and sclerotized ; anterior strut of gonangulum slender and sclerotized, posterior strut fused to paratergite IX with ventral end projecting well below edge of paratergite, forming a conspicuous fulcrum for the second gonocoxa ; gonoplacs small, flap-like and membranously united in midline ; median spermatheca present.

Cryptostemma alienum : similar to *Ceratocombus coleoptratus* in general structure; paratergites VIII and IX not separate from respective terga ; first gonocoxa almost completely membranous ; gonapophyses much shorter and less sclerotized ; gonoplacs fused to paratergites IX, appearing as ventral extensions of latter.

Saunders (1892) and Handlirsch (1908) placed the Dipsocoridae as a subfamily of the Cimicidae. Reuter (1912) erected a distinct series, the Trichotelocera, for this family and was followed by Oshanin (1916) and Pruthi (1925).

Pruthi (1925) stated that there was no similarity between the male genitalia of the Dipsocoridae and Cimicidae, but that there was a partial resemblance to the Reduviidae. Leston, Pendergrast and Southwood (1954), however, stated that the Dipsocoroidea were probably allied to the Cimicomorpha, and Stichel (1955) has placed the family in this division, in the Cimicoidea. Pendergrast (1957) has shown the Dipsocoridae to possess a true median spermatheca which has little affinity with that of other forms.

On the shape and structure of the gonapophyses, together with the possession of a median spermatheca and gonoplacs, this superfamily appears to be related to the Saldidae. The modification of the first gonocoxae, which appear to have fused to form an invaginated plate attached to sternum VII posteriorly, and the small size of the gonoplacs, distinguish this superfamily.

Reduvioidea

Reduviidae

Dr. N. T. Davis of the University of Connecticut is at present studying the female genitalia and systematics of this group. I have studied *Rhodnius prolixus* Stål in some detail, and an account of this is presented together with a few observations on other species.

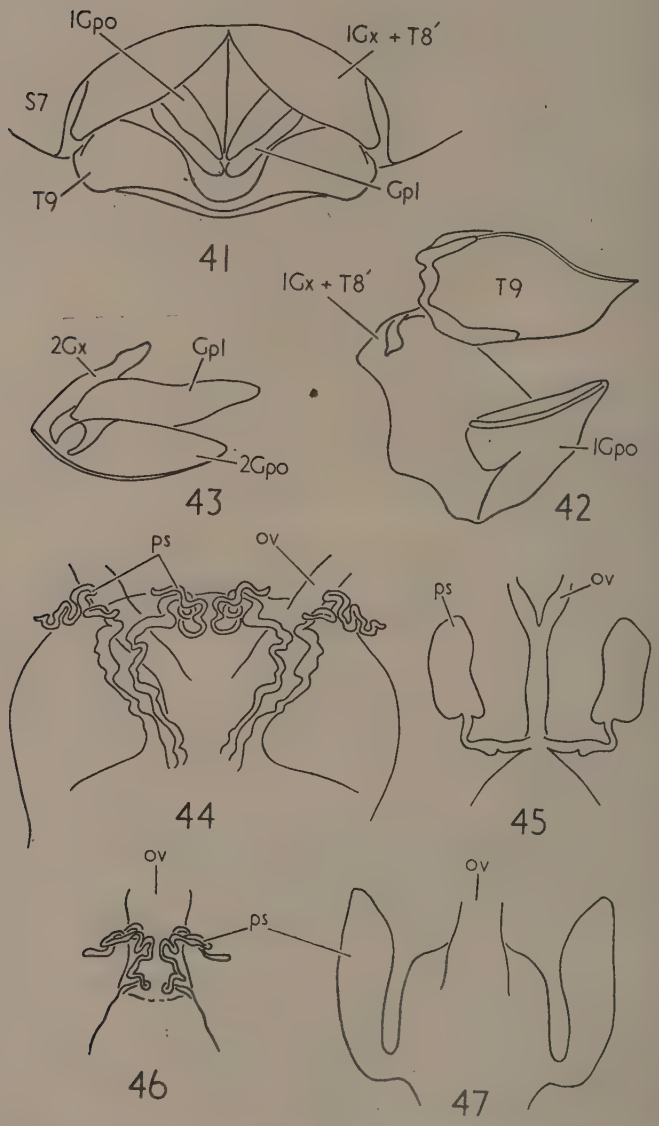
Previous descriptions : Davis, 1957 ; Galliard, 1935 ; Kershaw, 1909 ; Wigglesworth, 1948.

Species examined : *Rhodnius prolixus* Stål (figs. 41–43).

Posterior margin of sternum VII folded backwards and inwards and provided with muscles ; first gonocoxa fused completely with paratergite VIII, the non-functional spiracle VIII being found at dorsal edge of the fused structure ; paratergites IX large, rounded, not meeting in mid-line posteriorly and not separate from tergum IX ; first gonapophysis short, triangular and almost completely membranous ; rami sclerotized, short and interlocking ; anterior strut of gonangulum membranous ; second gonocoxa slender, sclerotized and articulating with ventral end of posterior strut of gonangulum, about third of way from distal end ; second gonapophysis broad, flattened and antero-medially with mesad projection ; second gonapophyses apically united and basally connected by continuation of inter-gonocoxal membrane ; gonoplacs broad and very similar to fused second gonapophyses in shape, united except at extreme apex and completely free from second gonocoxae ; genital chamber large and sac-like ; median spermathecal gland present ; a pair of lateral finger-like pseudospermathecae present ; ring sclerites absent.

The musculature of the female genitalia of *R. prolixus* is shown in figure 101. A conspicuous feature is the divided anterior dilator muscle of the genital chamber.

An examination of other species from various subfamilies of the Reduviidae shows a great variation in the structure of the median spermathecal gland and pseudospermathecae. This was also noted by Pendergrast (1957). He stated, however, that all the species of Reduviidae examined, and those described by other workers, have two pseudospermathecae (" spermathecae "). I have found a species of *Petalochirus* from Uganda to possess four pseudospermathecae (fig. 44). The median spermathecal gland is not present in all Reduviidae, but in some it is said to be paired (Kershaw, 1909). The types of pseudospermathecae, some of which are illustrated in figures 44–47, show the range of structure in the various subfamilies and suggest that they could be of great value as taxonomic characters in this group.



Figs. 41–47.—(41)–(43) *Rhodnius prolixus* Stål (Reduviidae): (41) ventral view of female terminalia; (42) first (43) second gonocoxa and associated parts; (44)–(47) pseudospermathecae of: (44) *Petalochirus* sp. (Reduviidae, Salyavatinae); (45) *Ischnobaena* sp. (Reduviidae, Emesinae); (46) *Ptilocnemus* sp. (Reduviidae, Holoptilinae); (47) *Glymmatophora* sp. (Reduviidae, Ectichodiinae).

Phymatidae

Previous description : Davis, 1957.
Species examined : *Phymata erosa* (L.).

A central and two lateral sclerites only visible from exterior, central being terga VIII and IX and the lateral the fused paratergites VIII and first gonocoxae, which appear as semicircular structures ; first gonapophyses very reduced, very small, membranous and flap-like structures at base of first gonocoxae, and attached to broad ventral membrane connecting the two first gonocoxae ; paratergites IX not separated from tergum IX ; two partially sclerotized, joined structures attached to tergum IX probably represent the second gonapophyses ; second gonocoxae either fused to tergum IX or absent ; gonoplacs apparently absent ; genital chamber large and sacciform with a median spermathecal gland and paired lateral pseudospermathecae as in *Rhodnius*.

The female genitalia in the Reduvioidea are of the plate-shaped type, oviposition taking place on the surface of the substratum and not usually in plant tissue. The median spermatheca serves as a secretory gland only and it is known as the colleterial gland when present, its secretion serving as an adhesive to attach the eggs firmly to the substratum. Paired lateral pseudospermathecae are usually present and receive and store sperm. There is a fusion of paratergite VIII and the first gonocoxa, spiracle VIII becoming nonfunctional ; gonoplacs are usually present.

The paired lateral pseudospermathecae are reminiscent of the lateral pouches present in many other groups of insects (*e.g.* Collembola, *Gryllotalpa*, Siphunculata, Megaloptera, *etc.* (Heberdey, 1931)). They may not be homologous throughout the Reduvioidea.

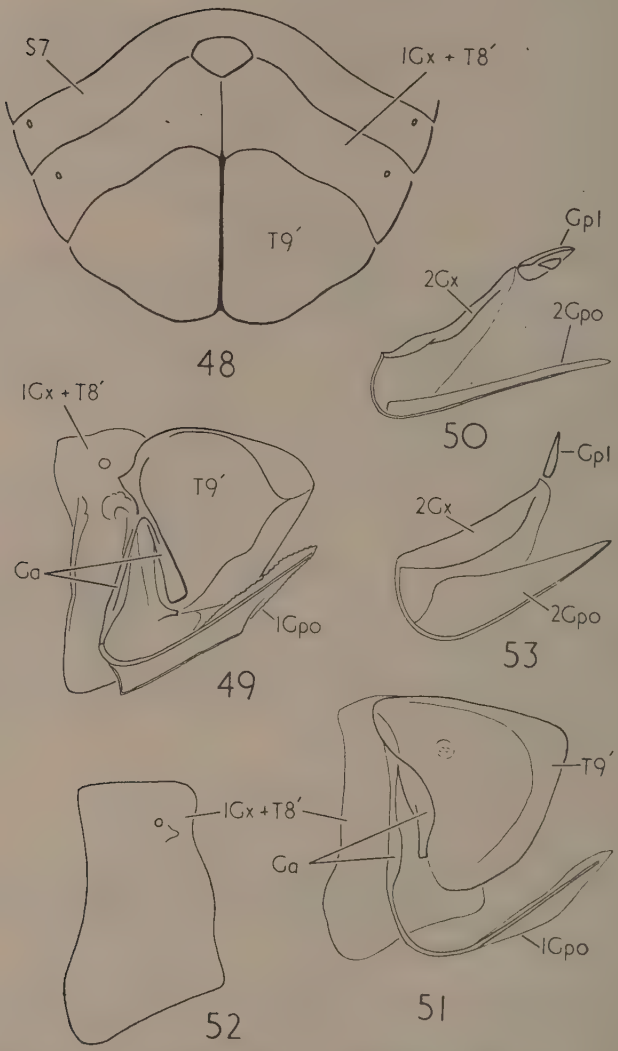
In the past there was considerable discussion regarding the families to be included in the Reduvioidea. The study of the female genitalia indicates that it should include only the Reduviidae and Phymatidae. Pendergrast (1957) has reviewed earlier groupings in this superfamiliy and has concluded that it should contain the Reduviidae and Phymatidae, with the Tingidae as a possible addition. The present work indicates that the Tingidae should be placed with the Vianaididae in a separate superfamily.

Tingoidea

Tingidae

Previous descriptions : Feldman and Bailey, 1952 ; Sharga, 1955.
Species examined : *Tingis reticulata* H.-S. (figs. 48–50), *T. cardui* (L.), *T. ampliata* (H.-S.), *Acalypta parvula* (Fall.), *Agramma laeta* (Fall.), *Corythuca padi* Drake.

Small triangular sclerite attached in mid-line to posterior margin of sternum VII and overlapping base of genitalia ; paratergites VIII fused to dorsal edge of first gonocoxae, but individuality of sclerites still recognisable ; paratergites IX large and conspicuous ; gonapophyses elongate, laciniate and sclerotized ; first gonapophyses united in basal part and terminally with serrate ridges ; second gonapophyses united but not ridged ; first gonocoxae postero-ventrally slightly produced ; second gonocoxae rather crescentic in shape and free from each other posteriorly ; gonoplacs present, each often composed of two separate sclerites ; gonangulum fused to paratergite IX at dorsal angle only, anterior strut long, slender and posterior strut free from paratergite IX, rather flat ; gonangulum



Figs. 48–53.—(48)–(50) *Tingis reticulata* H.-S. (Tingidae): (48) ventral view of female terminalia; (49) first (50) second gonocoxa and associated parts; (51)-(53) *Anommatocoris minutissimus* China (Vianaididae): (51) first gonocoxa and associated parts; (52) fused first gonocoxa and paratergite VIII; (53) second gonocoxa and associated parts.

at dorsal angle also fused to first gonocoxa and paratergite VIII, where the latter two sclerites fuse ; rami sclerotized and interlocking ; single ring sclerite present posteriorly in dorsal wall of genital chamber ; true median spermatheca absent ; paired sac-like pouches—pseudospermathecae—present anteriorly in genital chamber.

Vianaididae

Species examined : *Anommatocoris minutissimus* China (figs. 51–53), *Vianaida coleopterata* Korm.

Similar to Tingidae, but with genital chamber sacciform, large and without anterior sac-like pseudospermathecae ; ring sclerite absent ; gonoplacs present, but almost completely desclerotized ; fusion of paratergite VIII and first gonocoxa complete, with loss of individuality of sclerites ; posterior strut of gonangulum fused to paratergite IX ; gonangulum not fused to first gonocoxa + paratergite VIII ; conical projection on paratergite VIII incompletely fused to paratergite IX.

China (1945) described *Anommatocoris*, a new genus of Heteroptera, and placed it as an aberrant member of the subfamily Oxycareninae (Lygaeidae), the genus having lost the ventral abdominal trichobothria. Kormilev (1955*b*) erected a new family, the Vianaididae, for a new genus, *Vianaida*, and in this he also included *Anommatocoris*. Examination of the female genitalia enables the systematic position of these genera to be ascertained. In the fusion of paratergite VIII and the first gonocoxa, the presence of gonoplacs, the absence of a true median spermatheca and the presence of the triangular sclerite at the base of the genitalia, the family Vianaididae is found to be quite distinct from the Lygaeidae and close to the Tingidae. The drawings by the two authors of the female terminalia, seen from the exterior, are not alike. Kormilev has omitted to insert the line delimiting the fused first gonocoxa and paratergite VIII.

It appears that the Vianaididae is a good family close to the Tingidae, but my studies suggest that *Vianaida* and *Anommatocoris* are congeneric.

The female genitalia of the Tingoidea have a ventral aspect and appear rather flattened and plate-like, but a well developed laciniate ovipositor is present, eggs usually being laid in plant tissue. There is no median spermatheca, sac-like pseudospermathecae being present in the Tingidae. The latter family is unique in the Heteroptera examined, in having the posterior strut of the gonangulum not fused to paratergite IX, except at its dorsal angle. The first gonocoxa and paratergite VIII are fused and gonoplacs are present. The rami are sclerotized, complete and interlocking and there is a small triangular sclerite at the base of the ovipositor. There is also a connection between paratergite VIII and paratergite IX and/or the gonangulum.

Reuter (1912), China (1933), Börner (1934), Beier (1938) and Poisson (1951) considered the Tingidae and Piesmidae to be closely related. Tullgren (1918) was the first to show that these families were quite separate. Whilst the second possessed abdominal trichobothria, they were absent in the first. Subsequently, most studies have shown the Tingoidea, as previously constituted, to be an unnatural group. Leston (1953*b*) noted the similarity between the Tingid and Mirid egg. Leston, Pendergrast and Southwood (1954) suggested that the Tingidae were related to the Reduvioidea, but were unable to place the Piesmidae for certain in any superfamily of the Heteroptera Trichophora

of Tullgren. Pendergrast (1957) placed the Piesmidae in the same group as the Lygaeidae. As already stated, the Piesmidae can be placed in the Lygaeoidea on the structure of the female genitalia. The Tingidae, together with the Vianaididae, form a group here considered to warrant superfamily status.

Saldoidea

Saldidae

Previous descriptions : Ekblom, 1926 ; Leston, 1956*d* ; Snodgrass, 1933.

Species examined : *Salda littoralis* (L.) (figs. 54–56), *Saldula saltatoria* (L.), *Aepophilus bonnairei* Sign.

Paratergite VIII firmly united to dorsal edge of first gonocoxa ; individuality of sclerites associated in this fusion lost in *Aepophilus* ; paratergite IX not separated from tergum IX ; first gonapophyses joined by membrane, elongate and sclerotized, tips serrate on dorsal margin, each gonapophysis partially split longitudinally ; rami sclerotized and interlocking ; second gonapophyses sclerotized and united except at apex, terminally truncate and not tapering like first gonapophyses ; anterior strut of gonangulum rather short, broad and flattened ; second gonocoxa elongate, sclerotized, with dorsal edge thickened ; gonoplacs broad and flat, sclerotized and united by membrane, except proximally where united by sclerotized mesad projections ; gonoplacs not so united in *Aepophilus* ; single median spermatheca present.

Leptopodidae

Species examined : *Valleriola greeni* Dist. (figs. 59, 60), *Patapius spinosus* (Rossi).

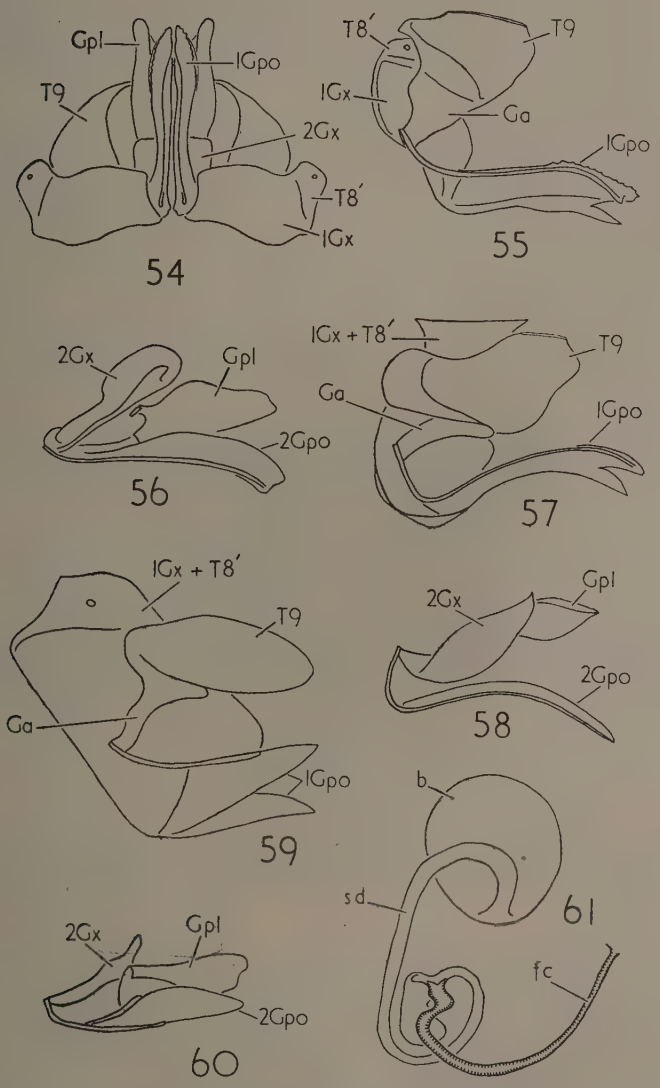
Sternum VII produced posteriorly and covering genitalia ; paratergites VIII fused to first gonocoxae, in *Valleriola* sclerites still distinct ; paratergites IX rounded posteriorly and separate ; first gonapophysis triangular and sclerotized and partially split longitudinally ; rami sclerotized and interlocking ; anterior strut of gonangulum short and partially sclerotized ; second gonocoxa slender and partially sclerotized ; second gonapophysis rather flattened and partially sclerotized, longer in *Valleriola* ; gonoplacs sclerotized, broad, flat but not united ; median spermatheca present ; wall of genital chamber surrounding opening of spermathecal duct with an elongate diamond-shaped sclerite.

Mesoveliidae

Previous descriptions : Ekblom, 1928 ; Neering, 1954.

Species examined : *Mesovelia furcata* Muls. and Rey (figs. 57, 58), *M. vittigera* Horv., *Mesoveloidea williamsi* Hungerf.

Anterior margin of sternum VII in mid-line produced antero-internally as a long apodeme; paratergite VIII completely fused to first gonocoxa ; first gonapophysis elongate, laciniate and sclerotized, with serrations ventro-laterally, each gonapophysis partially split longitudinally ; rami sclerotized and interlocking ; anterior strut of gonangulum rather broad and flat ; second gonocoxa elongate, broad and flat, sclerotized and with dorsal edge slightly thickened ; second gonapophyses elongate, sclerotized and laciniate, united except at apex and without serrations ; gonoplacs triangular in shape, sclerotized and attached to second gonocoxae, dorsal and ventral edges slightly curved mesad ; median spermatheca with accessory fecundation canal.



FIGS. 54–61.—(54)–(56) *Salda littoralis* (L.) (Saldidae) : (54) ventral view of female terminalia ; (55) first (56) second gonocoxa and associated parts ; (57)–(58) *Mesovelia furcata* Muls. and Rey (Mesoveliidae) ; (57) first (58) second gonocoxa and associated parts ; (59)–(60) *Valleriola greeni* Dist. (Leptopodidae) : (59) first (60) second gonocoxa and associated parts ; (61) *Leotichus speluncerum* China (Leotichidae) : spermatheca.

Esaki and China (1927) erected a group, the Telmatobia, to contain the Ochteridae, Galgulidae (= Gelastocoridae), Velocipedidae, Leptopodidae and Saldidae (includes Aepophilidae). Pendergrast (1957) has shown that this is not a natural group. He has removed the Ochteridae, Galgulidae and Velocipedidae and has stated that the Saldoidea should contain the Saldidae and Leptopodidae only. The study of the female genitalia supports this, but suggests that the Saldoidea should perhaps also include the Mesoveliidae. Pendergrast (1957) has shown that the Mesoveliidae possess a fecundation canal, as do the Hydrometridae, Hebridae, Gerridae and Veliidae. He has, therefore, considered these to represent a monophyletic group. However, there is a strong suggestion of convergence. I have found a fecundation canal to be present in *Leotichius speluncerus* China. In the Pentatomoidea, Leston has suggested that a structure, probably functioning as a fecundation canal, is present in *Hotea subfasciata*. If such a canal can arise by convergent evolution in these species, there is no reason to suppose that it could not arise independently in the Mesoveliidae and the other families mentioned. It has evolved independently in the Carabidae (Coleoptera) (Stein, 1847). Since the female genitalia are similar to those of the Saldidae and quite different from those of the Gerridae, Veliidae, *etc.*, the Mesoveliidae is here considered within the Saldoidea.

Pendergrast (1957) has further noted that the internal male genitalia of the Mesoveliidae possess accessory glands and thus they differ from the other families he considered to belong to the same group. He noted also that accessory glands (mesadenes) were present in the Saldidae.

The present study has also shown that the female genitalia of the Aepophilidae are extremely similar to those of the Saldidae, thus supporting the inclusion of this group within the Saldidae (Leston, 1956*d*).

The large gonoplacs, the fusion of paratergites VIII and the first gonocoxae and the partially divided and often serrate nature of the first gonapophyses appear to be characters distinguishing the Saldoidea.

Gerroidea

Veliidae

Previous description : Ekblom, 1926.

Species examined : *Velia caprai* Tam. (figs. 62–64), *V. sauli* Tam., *V. currens* (F.), *Microvelia reticulata* (Burm.), *M. pulchella* Westw., *Rhagovelia tenuipes* Champ. (fig. 65).

Tergum IX forming an anal plate or lid covering posterior of abdomen and obscuring genitalia in *Velia* spp., but only partially so in *Microvelia* spp.; in *Rhagovelia* tergum IX not forming an anal lid ; sternum VII anteriorly produced as an apodeme in mid-line, extending to anterior margin of sternum VI ; first gonocoxa and paratergite VIII fused ; first gonapophyses elongate, laciniate and sclerotized ; rami sclerotized and interlocking ; second gonapophyses elongate, laciniate and sclerotized, united by a Y-shaped sclerotized bar about one third of way from base in *Velia* spp.; second gonapophyses covered with hairy projections apically ; gonangulum more or less triangular in shape with posterior angle elongately produced posteriorly and fused to paratergite IX, which is very small ; second gonocoxae sclerotized and elongate, very closely associated with gonangulum and paratergite IX ; gonoplacs absent ; median spermatheca with an accessory fecundation canal.

Hebroveliidae

Previous description : Lundblad, 1939.
Species examined : *Hebrovelia singularis* Lundbl.

Identical in structure with Veliidae, but with tergum IX not forming an anal lid ; genitalia externally appearing as in *Rhagovelia*, with first gonocoxae visible.

Macroveliidae

Species examined : *Macrovelia horni* Uhl., *Ocellovelia germari* Dist.
Female genitalia as in Hebroveliidae.

Gerridae

Previous descriptions : Carpenter, 1906 ; Ekblom, 1926 ; Guthrie, 1954 ; Imms, 1936.
Species examined : *Gerris najas* (Deg.) (figs. 66, 67), *G. notabilis* D. & H., *G. incurvatus* D. & H., *G. lacustris* (L.), *G. gibbifer* Schum., *Brachymetra albinervis* A. & S., *Cylindrostethus productus* Spin.

Almost identical with Veliidae ; with apodeme of sternum VII longer ; tergum IX not forming an anal lid ; second gonapophyses without feathery projections ; apodeme of first gonocoxae smaller and narrower ; second gonocoxae and gonoplacs absent.

Hydrometridae

Previous descriptions : Ekblom, 1926 ; Sprague, 1956.
Species examined : *Hydrometra stagnorum* (L.) (figs. 68, 69).

Tergum IX forming an anal lid ; anterior margin of sternum VII in mid-line produced as an apodeme ; paratergite VIII ventrally completely united with first gonocoxa ; first gonapophysis small, triangular and sclerotized ; small portion of rami at base of gonapophyses sclerotized and interlocking, otherwise membranous ; anterior strut of gonangulum membranous ; second gonapophysis triangular and membranous ; second gonocoxa quadrate in shape and sclerotized posteriorly, the anterior projection connecting with second gonapophysis, almost completely membranous ; gonoplacs apparently absent ; median spermatheca with accessory fecundation canal.

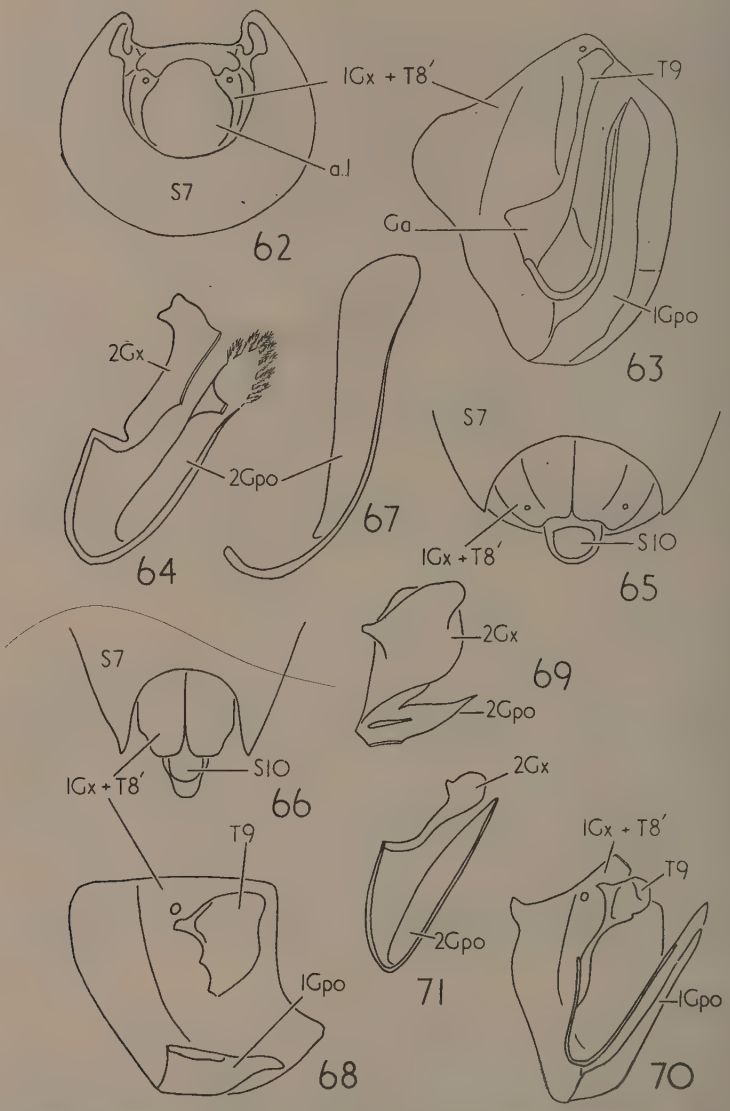
I consider the female genitalia to be of the laciniate type and not the plate-shaped type, as stated by Dupuis (1955).

Hebridae

Species examined : *Hebrus ruficeps* (Thoms.) (figs. 70, 71).

Tergum IX not forming an anal lid ; paratergite VIII fused with first gonocoxa ; gonapophyses partially sclerotized, elongate and with sclerotized and interlocking rami ; anterior strut of gonangulum partial, sclerotized ; paratergite IX and second gonocoxa about same size, quadrate in shape and sclerotized ; paratergite IX sclerotized posteriorly only ; gonoplacs absent ; median spermatheca with accessory fecundation canal.

McKinstry (1942) has given a table of characters separating the families here considered in the Gerroidea. He also included the Mesoveliidae, but this has already been considered in the Saldoidea. China and Usinger (1949) have



Figs. 62–71.—(62)–(64) *Velia caprai* Tam. (Veliidae): (62) posterior view of female terminalia; (63) first (64) second gonocoxa and associated parts; (65) *Rhagovelia tenuipes* Champ. (Veliidae): ventral view of female terminalia; (66)–(67) *Gerris najas* (Deg.) (Gerridae): (66) ventral view of female terminalia; (67) second gonapophysis; (68)–(69) *Hydrometra stagnorum* (L.) (Hydrometridae): (68) first (69) second gonocoxa and associated parts; (70)–(71) *Hebrus ruficeps* (Thoms.) (Hebridae): (70) first (71) second gonocoxa and associated parts.

reduced the Hebroveliidae and Macroveliidae to subfamily rank within the Veliidae. The present work has shown that, whereas the Veliinae have tergum IX forming an anal lid, the Microveliinae have the terminalia only partially obscured by tergum IX and the Rhagoveliinae are without an anal lid. If these three subfamilies are retained within the Veliidae, there appears no reason why the Hebroveliidae and Macroveliidae should not also be included. The anal lid character has not been used in the systematics of this group. It appears to be a very reliable character and warrants further study.

China (1957) has given a summary of characters separating the Veliidae and Gerridae. To this may be added the loss of the second gonocoxae in the Gerridae and the presence of feathery projections on the gonapophyses in some Veliidae. The second gonocoxa is present in the Veliidae and not absent, as stated by Ekblom (1926).

Pendergrast (1957) has shown the Gerroidea (including the Mesoveliidae) to be distinct from all other Heteroptera in possessing a fecundation canal.

Nepoidea

Nepidae

Previous descriptions : Berlese, 1909 ; Dufour, 1821 ; Hamilton, 1931 ; Larsen, 1938 ; Locy, 1884 ; Marshall and Severin, 1904 ; Verhoeff, 1893.

Species examined : *Nepa cinerea* L. (figs. 72, 73).

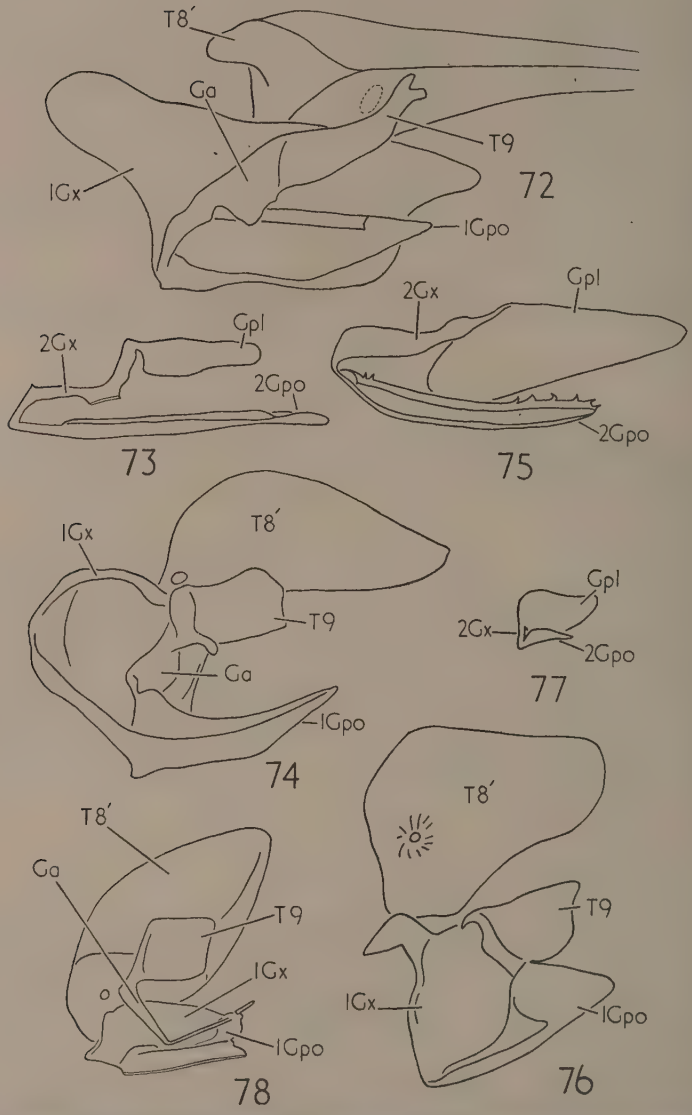
Sternum VII produced posteriorly, covering genitalia ; paratergite VIII elongate, projecting beyond end of abdomen and forming a respiratory siphon ; paratergite IX rather small, elongate and not separate from tergum IX ; first gonocoxa quadrate with antero-dorsal angle produced anteriorly as a long broad apodeme ; first gonapophysis broad, elongate and sclerotized ; sclerotized rami on dorsal edge of first gonapophyses on basal two-thirds ; gonangulum triangular in shape, sclerotized and fused to paratergite IX posteriorly ; second gonapophyses elongate, sclerotized and fused at base ; second ramus extending along basal two-thirds of second gonapophysis and interlocking with first ramus ; second gonocoxa slender, curved dorsally in posterior half and joined by sclerotized bridge across middle with opposite number ; gonoplac sclerotized and rather stylus-like ; single median spermatheca present.

Belostomatidae

Species examined : *Lethocerus grandis* (F.).

Paratergite VIII elongate, projecting beyond end of abdomen and forming a respiratory siphon ; paratergite IX small and quadrate ; first gonocoxa triangular and slightly produced posteriorly ; antero-dorsal corner of first gonocoxa produced as a short, broad apodeme ; first gonapophysis slender, elongate, triangular in shape, sclerotized and with a distinct shallowly grooved ramus ; anterior strut of gonangulum slender and sclerotized ; gonoplac rather stylus-like ; single median spermatheca present.

Börner (1934) and Pendergrast (1957) considered the Nepoidea to contain only the Nepidae and Belostomatidae, whereas Esaki and China (1927), Beier (1938) and Poisson (1951) include the Naucoridae and Aphelocheiridae also. The study of the female genitalia supports the conclusions reached by Börner and Pendergrast. They are characterised by the very long paratergites VIII forming a respiratory siphon and the stylus-like gonoplacs.



FIGS. 72–78.—(72)–(73) *Nepa cinerea* L. (Nepidae): (72) first (73) second gonocoxa and associated parts; (74)–(75) *Ilyocoris cimicoides* (L.) (Naucoridae): (74) first (75) second gonocoxa and associated parts; (76)–(77) *Aphelocheirus montandoni* Horv. (Aphelocheiridae): (76) first (77) second gonocoxa and associated parts; (78) *Sigara dorsalis* Leach (Corixidae): first gonocoxa and associated parts.

Naucoroidea

Naucoridae

Previous descriptions : Heymons, 1899 ; Larsen, 1938 ; Rawat, 1939.
Species examined : *Ilyocoris cimicoides* (L.) (figs. 74, 75).

Paratergite VIII large, broad and flattened, free from first gonocoxa ; first gonocoxa almost triangular in shape, with a broad apodeme antero-dorsally ; first gonapophysis laciniate, sclerotized with a well defined grooved ramus ; anterior strut of gonangulum broad, flat and sclerotized ; second gonapophysis long, slender and sclerotized with short blunt spines apically and with a distinct ridged ramus ; second gonocoxa flat, narrow and elongate ; gonoplac broad and flat, subequal to paratergite VIII ; single median spermatheca present.

Aphelocheiridae

Previous description : Larsen, 1938.
Species examined : *Aphelocheirus montandoni* Horv. (figs. 76, 77).

Paratergite VIII large, broad and flattened, not fused to first gonocoxa ; first gonocoxa rather quadrate in shape with an elongate apodeme antero-dorsally ; first gonapophysis short and triangular and all but fused to paratergite IX ; anterior strut of gonangulum apparently absent ; second gonapophyses very small and fused and without rami ; second gonocoxa very small and slender ; gonoplac quite large and flat, about as large as paratergite IX ; single median spermatheca present.

The genitalia of the Aphelocheiridae I consider to be of the laciniate and not the plate-shaped type, as stated by Dupuis (1955).

The two families here considered in the Naucoroidea were included in the Notonectoidea by Oshanin (1916), Pruthi (1925), Börner (1934) and Stichel (1955). Esaki and China (1927), Beier (1938) and Poisson (1951) have included them in the Nepoidea. Esaki and China (1927) did, however, consider the Naucoridae and Aphelocheiridae more closely related to each other than to either the Nepidae or Belostomatidae.

The Nepidae and Belostomatidae have already been considered. Pendergrast (1957) found that the Naucoridae and Aphelocheiridae, together with the Corixidae and Ochteridae, could be grouped together on the evidence of the spermatheca.

The study of the female genitalia suggests that the Naucoroidea should contain only the Naucoridae and Aphelocheiridae. The structure of the gonoplacs and paratergites VIII, with the reduced second gonocoxae and gonangulum, characterise the superfamily.

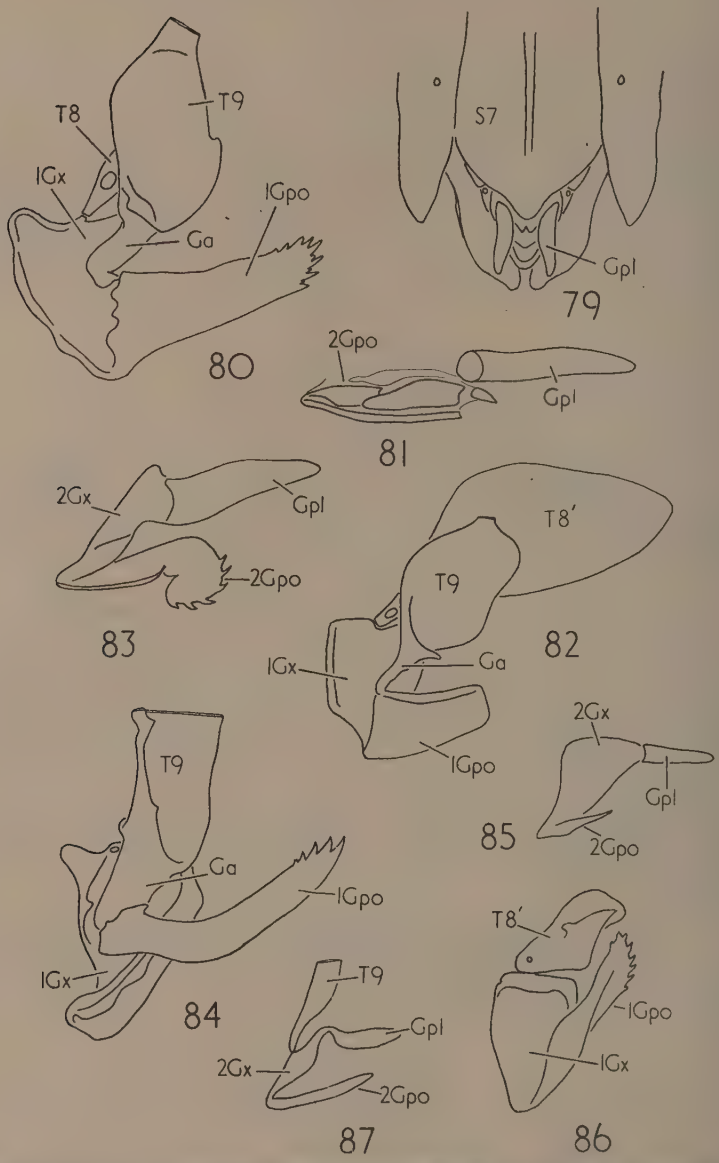
Notonectoidea

Notonectidae

Notonectinae

Previous descriptions : Berlese, 1909 ; Larsen, 1938.
Species examined : *Notonecta glauca* L. (figs. 79–81), *N. undulata* Say, *Enithares lineatipes* Horv. (figs. 82, 83).

Sternum VII produced posteriorly, partially covering genitalia ; paratergite VIII large and conspicuous, with spiracle VIII close to attachment with first gonocoxa ; paratergite



FIGS. 79–87.—(79)–(81) *Notonecta glauca* L. (Notonectidae): (79) ventral view of female terminalia; (80) first (81) second gonocoxa and associated parts; (82)–(83) *Enithares lineatipes* Horv. (Notonectidae): (82) first (83) second gonocoxa and associated parts; (84)–(85) *Buenoa antigone* Kirk. (Notonectidae): (84) first (85) second gonocoxa and associated parts; (86)–(87) *Plea atomaria* (Pall.) (Pleidae): (86) first (87) second gonocoxa and associated parts.

IX smaller and not separated from tergum IX ; first gonocoxa almost triangular in shape, anterior margin thickened, but without projecting apodeme ; first gonapophysis rather broad and sclerotized, with spines at apex ; first rami indistinct ; gonangulum triangular in shape and sclerotized ; second gonocoxa slender and only partially sclerotized ; second ramus present and sclerotized ; second gonapophysis sclerotized—in *Notonecta* consisting of two separate sclerites, in *Enithares* heavily sclerotized throughout, bent ventrally at apex and with spines ; gonoplacs separate and stylus-like ; single median spermatheca present.

Anisopinae

Species examined : *Anisops niveus* (F.), *Buenoa antigone* Kirk. (figs. 84, 85), *B. pallens* Champ.

Sternum VII produced posteriorly as in *Notonecta* ; paratergite VIII fused to first gonocoxa and spiracle VIII located on extreme dorsal edge of latter ; paratergite IX rather membranous ; first gonocoxa triangular in shape, with posterior margin swollen, reflexed and heavily sclerotized ; antero-dorsal corner of first gonocoxa produced forward as an apodeme ; first gonapophysis heavily sclerotized, as an elongate, curved rod with spines apically ; rami absent ; gonangulum triangular in shape, heavily sclerotized, posteriorly fused to paratergite IX and extending dorsally to meet its opposite number in mid-line ; second gonocoxa rather membranous ; second gonapophyses united at base, very short, laciniate and membranous ; gonoplacs separate, short and stylus-like ; single median spermatheca present.

The female genitalia of the two subfamilies considered here appear to be quite different and distinctive, supporting the divisions of the family adopted at present. The structure in the Anisopinae appears to be the more specialised.

Pleidae

Previous description : Wefelscheid, 1912.
Species examined : *Plea atomaria* (Pall.) (figs. 86, 87).

Abdominal sterna keeled in mid-line ; sternum VIII large and covering genitalia ; paratergite VII produced posteriorly ; paratergite VIII rather large, not fused to first gonocoxa ; paratergite IX much smaller than paratergite VIII and not separated from tergum IX ; first gonocoxa rather triangular in shape, larger than paratergite VIII and anterior margin without projecting apodeme ; first gonapophysis rather broad and sclerotized, apically armed with sclerotized teeth ; first ramus indistinct ; anterior strut of gonangulum absent ; second gonocoxa crescentic in shape ; second gonapophyses much smaller than first and united ; gonoplacs separate and rather stylus-like ; single median spermatheca present.

Reuter (1912), Oshanin (1916) and Pruthi (1925) included the Notonectidae, Naucoridae, Nepidae and Belostomatidae in this group. Börner (1934) considered the Notonectoidea to contain the Naucoridae, Aphelocheiridae, Notonectidae and Pleidae. Stichel's (1955) Notonectoidea contains the Pleidae, Notonectidae, Naucoridae, Belostomatidae, Nepidae and Ranatridae. The position of the Nepidae (including the Ranatridae), Belostomatidae, Naucoridae and Aphelocheiridae has already been discussed. Pendergrast (1957) has suggested a redefinition of the Notonectoidea to include the Notonectidae, Pleidae, Helotrephidae and Galgulidae.

The study of the female genitalia suggests that only the Pleidae and Notonectidae should be included in this superfamily. However, although the Galgulidae and Helotrephidae do not appear to be allied to these two families, it has been found impossible to place them in any other superfamily on the structure of the female genitalia.

Ochteroidea

Ochteridae

Previous description : Jaczewski, 1934.

Species examined : *Ochterus marginatus* (Latr.) (figs. 88, 89).

Sternum VII produced posteriorly, with posterior margin indented in mid-line ; paratergite VIII not fused to first gonocoxa, indistinctly separated from tergum VIII which is divided into two mid-dorsally ; antero-ventral angle of paratergite VIII elongately produced ; paratergites IX quadrate in shape and very weakly sclerotized ; first gonocoxa quadrate with a very large finger-like anteriorly projecting apodeme ; first gonapophysis triangular and sclerotized ; rami sclerotized and interlocking ; rather straight and first ramus with groove rather shallow ; anterior strut of gonangulum slender and sclerotized ; second gonocoxa slender, sclerotized with dorso-posterior margin, except extreme apex, fused to ventral margin of paratergite IX ; gonoplacs rectangular in shape ; single median spermatheca present.

Paratergite VIII in *Ochterus* is similar to that in the Notonectidae ; Jaczewski (1934) stated that the female genitalia were reminiscent of those of Notonectidae, but the ovipositor is not as reduced as he indicated. The gonoplacs are similar to those in the Saldidae ; the first gonapophysis and gonocoxa are different from those in the Saldidae and appear quite distinctive.

Reuter (1912) included the Ochteroidea in his division Hydrobiotica and placed in it three families, Ochteridae, Galgulidae and Peloridiidae, the latter being set apart from the two former. Oshanin (1916) and Pruthi (1925) followed this scheme and included only the Ochteridae and Galgulidae. The Peloridiidae were placed in a new series of Hemiptera, the Coleorrhyncha, by Myers and China (1929) and this is placed in the Homoptera on the same status as the Auchenorrhyncha. A study of the female genitalia of *Hemiodoecus fidelis* Evans leads me to the same general conclusion, although it is not possible to draw a sharp distinction between the type of ovipositor in the Homoptera as distinct from the Heteroptera.

Corixoidea

Corixidae

Previous descriptions : Crampton, 1929 ; Griffith, 1945 ; Hagemann, 1910 ; Höregott and Jordan, 1954 ; Larsen, 1938 ; Poisson and Jaczewski, 1928.

Species examined : *Corixa punctata* (Ill.), *Sigara dorsalis* Leach (figs. 78, 90, 91).

Tergum VIII divided in mid-line ; paratergites VIII very large and carrying spiracles ; sternum VIII more or less undivided ; first gonapophyses finger-like and each bearing a stylus-like structure ; anterior strut of gonangulum present ; second gonocoxae probably

membranous and fused to second gonapophyses ; second gonapophyses rather large and meeting beneath anus, but not fusing in mid-line ; gonoplacs absent ; single median spermatheca present.

Crampton (1929) considers the stylus-like structure at the apex of the first gonapophysis to be a true gonostyle. The anterior strut of the gonangulum is called the S-shaped strut by Larsen (1938).

The female genitalia in this group are very characteristic and fairly constant in structure.

Börner (1904) erected the group Sandaliorrhyncha for the Corixidae. Many later authors have considered this family to be separate from the rest of the Heteroptera. China (1955*b*) has given a full survey of the systematic position of the Corixidae and states that he at one time considered that they might even be aquatic Homoptera.

On the structure of the female genitalia it would appear that the Corixidae should be placed quite apart from the rest of the Heteroptera.

Incertae sedis I

This group includes families with genitalia having Cimicoid affinities, but which cannot be placed in any of the present superfamilies on the structure of these organs.

Leotichidae

Species examined : *Leotichus speluncerum* China (figs. 61, 94, 95).

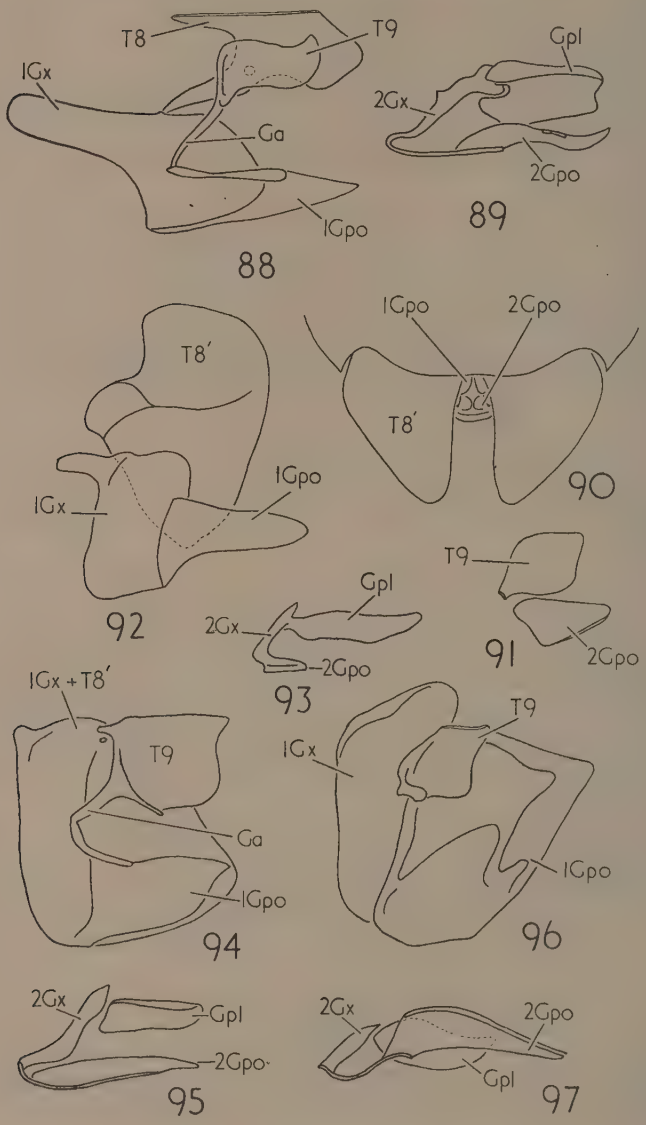
Paratergite VIII completely fused with first gonocoxa ; paratergite IX rounded posteriorly and separate from opposite number ; first gonapophysis broad and almost triangular in shape and heavily sclerotized ; rami sclerotized and interlocking ; anterior strut of gonangulum slender and sclerotized ; second gonapophysis elongate and sclerotized ; gonoplacs elongate rectangular and not united ; median spermatheca with accessory fecundation canal.

China (1933) when he erected this family placed it close to the Saldidae. Whilst there appear to be many characters supporting this systematic placing, the structure of the female genitalia, especially the nature of the first gonapophyses, does not concur. However, there is little doubt that the Leotichidae should be placed with the other aquatic Heteroptera. Pendergrast (1957) did not examine the spermatheca of the Leotichidae. In *Leotichus speluncerum* (fig. 61) I have found a median spermatheca with an accessory fecundation canal. Pendergrast would thus have included this family in the Amphibicorisae ; he would not have related it to the Saldidae as the latter lack such a canal. The structure of this canal in the Leotichidae is very similar to that in the Hebridae ; the female genitalia are quite unlike those of the Hebridae.

Helotrephidae

Species examined : *Neotrephus usingeri* China (figs. 96, 97).

Paratergite VIII not fused to first gonocoxa and not separated from tergum VIII ; first gonocoxa and first gonapophysis both triangular in shape, sclerotized and about same



FIGS. 88–97.—(88)–(89) *Ochterus marginatus* (Latr.) (Ochteridae): (88) first (89) second gonocoxa and associated parts; (90)–(91) *Sigara dorsalis* Leach (Corixidae): (90) ventral view of female terminalia; (91) second gonapophysis and associated parts. (92)–(93) *Nertha grandicollis* Germ. (Galgulidae): (92) first (93) second gonocoxa and associated parts; (94)–(95) *Leotichus speluncerum* China (Leotichidae): (94) first (95) second gonocoxa and associated parts; (96)–(97) *Neotrephus usingeri* China (Helotrephidae): (96) first (97) second gonocoxa and associated parts.

size ; first ramus and anterior strut of gonangulum membranous ; second gonocoxa small, elongate, rectangular and partially sclerotized ; paratergite IX fused to posterior strut of gonangulum which attaches to proximal end of second gonocoxa ; second ramus almost membranous ; second gonapophyses sclerotized and united dorsally, edges curved round ventrally to form an incomplete cone, extreme apices free ; gonoplacs rather large, sclerotized, free and somewhat stylus-like ; median spermatheca present.

China (1933, 1955*a*, 1955*b*) grouped the Helotrephidae with the Pleidae and Notonectidae. Pendergrast (1957), after a study of the spermatheca, supported this. The female genitalia of *Neotrephus* are unlike those in the latter two families, but they are also unlike those in any other family, although they clearly have some characters of the aquatic bugs.

Galgulidae

Species examined : *Nertha grandicollis* Germ. (figs. 92, 93).

Paratergite VIII free from first gonocoxa, prism-shaped with posterior angle produced ; first gonapophysis finger-like and sclerotized, larger than gonoplac ; rami and anterior strut of gonangulum membranous ; posterior strut of gonangulum fused to partially sclerotized paratergite IX ; second gonocoxa small rectangular in shape and partially sclerotized ; second gonapophyses united in mid-line and to inter-gonocoxal membrane, not projecting as valves posteriorly ; gonoplacs sclerotized, elongate and rectangular, not united ; median spermatheca present.

As stated when discussing the Ochteroidea, the female genitalia of *Nertha* do not appear similar to those of *Ochterus*, although they fall within the type of structure present in many of the water bugs.

Incertae sedis II

This group includes families which have the female genitalia so specialised as to make any systematic placing based on this structure impossible. In almost all cases an ovipositor is absent.

Aneuridae

Species examined : *Aneurus laevis* (F.), *A. avenius* (Duf.).

In this family it is not possible to trace any structures of the female genitalia. The ovipositor and associated sclerites are absent. There is no sign of the typical median spermatheca, but there is a simple small diverticulum in the dorsal wall of the genital chamber. Pendergrast (1957) states that this diverticulum is surrounded by tall glandular cells and that the sperm lies within this sac and in the anterior part of the chamber.

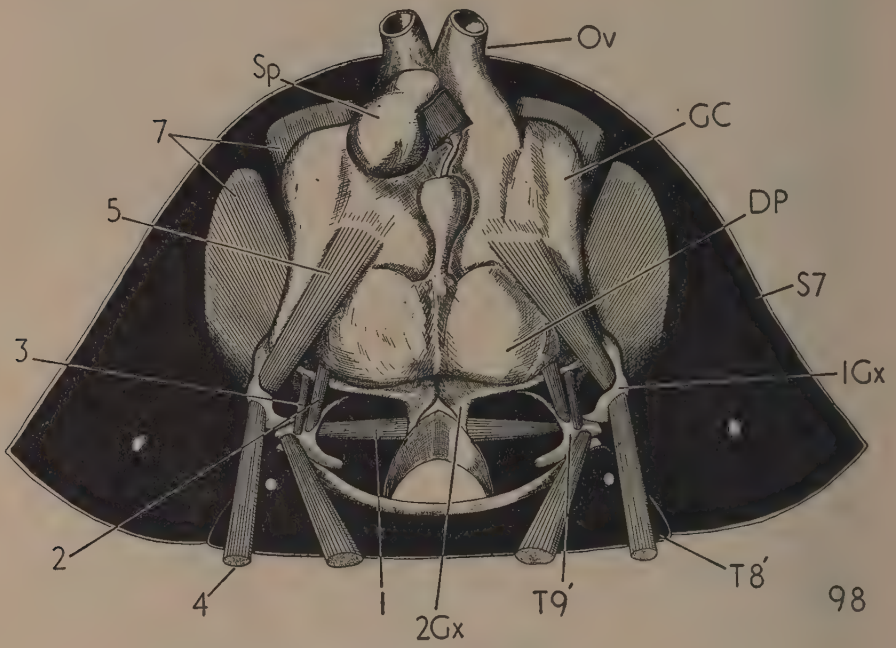
Leston, Pendergrast and Southwood (1954) point out that a true spermatheca is absent in *Aneurus* ; this is a Cimicoid character. However, Southwood (1956*a*) has shown that the structure of the egg is Pentatomoid in nature, with micropylar processes. All recent authors include the Aneuridae in the Aradoidea.

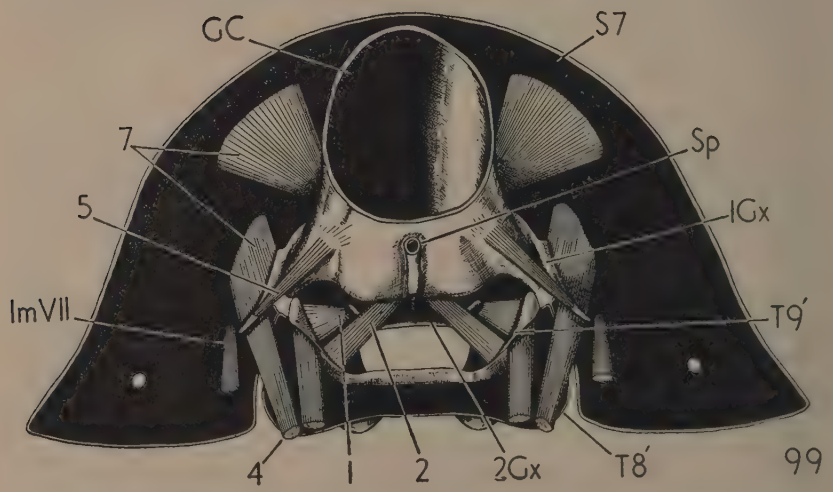
Enicocephalidae

Previous description : Carayon, 1950*a*.

Species examined : undetermined species from New Guinea.

Because of extreme reduction, an interpretation of the female genitalia of this family has proved so difficult that the account here given is very brief.





FIGS. 98–99.—Internal view of musculature of female terminalia of: (98) *Sehirus bicolor* (L.) (Cydnidae); (99) *Picromerus bidens* (L.) (Pentatomidae).

There is what appears to be a paratergite IX and three ventral sclerites, the homology of which cannot be ascertained on present information. A single median spermatheca is absent.

Carayon (1950*a*) has noted a small median seminal receptacle. Pendergrast (1957) has stated that this would indicate that the family was not allied to the Reduviidae. Leston, Pendergrast and Southwood (1954) have stated that the Enicocephalidae are apparently Geocorisae, but have pointed out that the wing venation suggests a distinct relationship with the Hydrocoridae. Stichel (1955) has erected a division, the (H) Enicocephalomorpha, for the Enicocephalidae, a group to be of equal status with the Pentatomomorpha and Cimicomorpha, but the female genitalia do not appear to help in the elucidation of this problem.

Schizopteridae

Species examined : *Schizoptera* sp.

In this family an ovipositor is apparently absent, but a true median spermatheca is present. The latter is an invaluable taxonomic character (Wygodzinsky, 1950).

This family is placed with the Dipsocoridae in the Dipsocoroidea, but this appears to be based solely on superficial resemblances.

Termitaphididae

Species examined : *Termitaphis* sp., *Termitaradus* sp.

This family is without an ovipositor. China (1955*a*) places it with the Aradidae.

Joppeicidae

Species examined : *Joppeicus paradoxus* Put.

An ovipositor is apparently absent in this family. China (1955*a*) has considered the systematic position and morphology of the Joppeicidae and concluded that it is closely related to the Reduviidae.

VI. Historical Account of the Classification of the Heteroptera

Kiritshenko (1951) has adequately compared the various classifications of the Heteroptera proposed prior to 1950 ; this will not be repeated here.

Leston, Pendergrast and Southwood (1954), in a consideration of the higher classification of the Geocorisae, recognised two distinct groups, the Pentatomomorpha and the Cimicomorpha. This was based on a study and re-evaluation of the male genitalia, abdominal trichobothria, wing venation, spermatheca, salivary glands and egg structure. Their Pentatomomorpha coincides with Pruthi's (1925) Pentatomid-type male genitalia group and with Tullgren's (1918) Heteroptera trichophora. China (1955*a*) expressed doubts on the validity of this division of the Geocorisae into two, but he adopts a similar division himself in his phylogenetic diagram in the same paper.

Stichel(1955) considers that there are five divisions of the Heteroptera ; these he calls the Hydrocoriomorpha, Amphibicoriomorpha, Henicocephalomorpha,

Cimicomorpha and Pentatomomorpha. I have elsewhere (Scudder, 1956*a*) commented on the naming of these divisions.

China (1955*b*) has discussed the evolution of the Amphibicorisae and Hydrocorisae and their relationships. Pendergrast (1957) has shown, by a study of the spermatheca, that the Amphibicorisae appear to be a monophyletic group, all possessing an accessory fecundation canal.

Many families have been continually moved from one division to another in the classifications and a large number of authors have made suggestions on the relationships of odd families. For example, Sahlberg (1920) and Ekblom (1928) removed the Hebridae and Mesoveliidae from the Anonycha, where they were placed by Reuter (1912) and placed them in the Amphibicorisae. The Saldidae seem always to have been a problem to the systematists and Leston, Pendergrast and Southwood (1954) and Southwood (1956*a*) were unable to place this family with any conviction; Leston and Scudder (1956) placed it in the Geocorisae, but China (1955*b*) considered it correctly placed in the Amphibicorisae.

VII. The Female Genitalia and Classification of the Heteroptera

The families in the foregoing account have been arranged, as far as possible, under superfamilies. A discussion or summary of the type of structure within each superfamily is given where possible.

The type of ovipositor appears to be dependent on the oviposition site and habit. Those ovipositing in plants, etc., have a laciniate type of ovipositor with lanceolate gonapophyses and the anterior strut of the gonangulum present and heavily sclerotized, whilst those ovipositing on the surface of leaves, trunks, etc., have a plate-shaped type of ovipositor with flap-like gonapophyses and the anterior strut of the gonangulum reduced and often completely membranous or absent. It is found that, within limits, the type and structure of the ovipositor is constant within the lower groups (*e.g.* superfamily or family), as members of these categories usually have the same oviposition habit. Thus the ovipositor can be employed, with other characters, in the delimiting of families and superfamilies. An example of this has already been published (Scudder, 1957*a*).

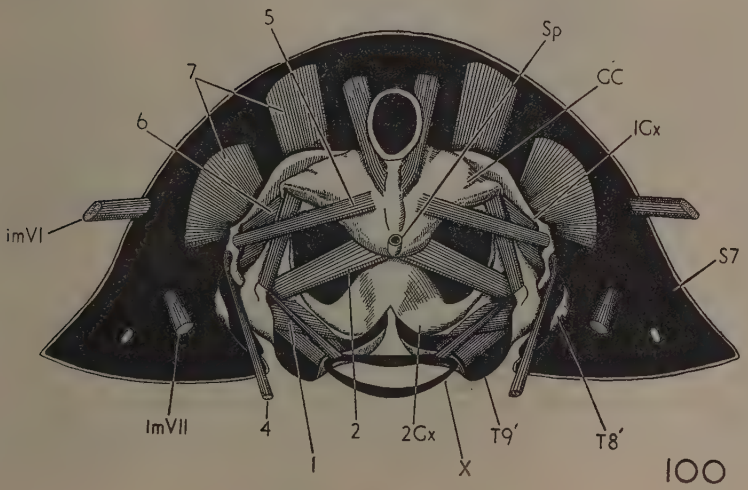
A survey of the superfamilies, excluding the Corixoidea and the " Incertae sedis II ", shows that, on the basis of the female terminalia, they fall into two apparently distinct groups. No single character satisfactorily indicates this grouping, but a complex of characters is present: their separation is expressed as below.

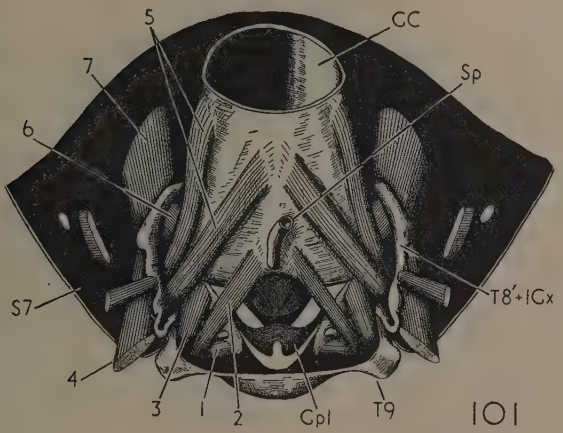
(i) Gonoplac always absent; no fusion of paratergite VIII and first gonocoxa; single median spermatheca present and functioning as a sperm-receiving and storage organ; pseudospermathecae absent; fecundation normal . Pentatomoidea, Coreoidea, Lygaeoidea, Aradoidea, Pyrrhocoroidea

(ii) Gonoplac usually present; paratergite VIII often fused with first gonocoxa; median spermatheca present or absent, if present sometimes functioning as in (i), at other times losing its functions of receiving and storing sperm and serving as a secretory organ; pseudospermathecae sometimes present; fecundation generally normal, but haemocoelic fecundation occasionally occurring
Cimicoidea, Reduvioidea, Tingoidea, Saldoidea, Dipsocoroidea, Gerroidea, Notonectoidea, Nepoidea, Naucoroidea, Ochteroidea, Incertae sedis I.

It will be seen that the grouping based on the female genitalia coincides, more or less, with that based by Pruthi (1925) on the male genitalia.

Southwood (1956*b*) has shown that the Pentatomomorpha have characteristically a tubular type of accessory salivary gland and usually a convoluted or coiled accessory duct, whereas the Cimicomorpha have a vesicular type of accessory salivary gland and a rather straight accessory duct. Dissections of





Figs. 100–101.—Internal view of musculature of female terminalia of: (100) *Dysdercus fasciatus* Sign. (Pyrrhocoridae); (101) *Rhodnius prolixus* Stål (Reduviidae).

several members of the Amphibicorisae and Hydrocorisae, together with the account by Baptist (1941), show that the salivary gland characters may be extended to the aquatic and semi-aquatic Heteroptera. The Amphibicorisae and Hydrocorisae have accessory salivary glands and ducts as in the Cimicomorpha. These two water-bug groups are also without ventral abdominal trichobothria and thus similar to Cimicomorpha.

Leston, Pendergrast and Southwood (1954) and Pendergrast (1957) state that the spermatheca is absent in the Cimicomorpha. As stated above, a homologue is present, but is usually modified as a secretory organ, the functions of receiving and storing sperm being usually taken over by analogous accessory structures, the pseudospermathecae.

The Cimicomorpha, as now defined, does not always have the true median spermatheca non-functional as such. It is feasible to consider the more primitive members as possibly having a functional spermatheca, or, conversely, to consider the modifications seen in most terrestrial Cimicomorpha as special features. There is ample evidence to suggest that a typical feature of certain land Cimicomorpha is the anomalous method of fecundation. Further, the pseudospermathecae throughout this division are not homologous. It does not seem inconsistent, therefore, to include the Amphibicorisae and Hydrocorisae (excluding Corixoidea) within the Cimicomorpha.

The female genitalia and the many other characters of the Corixoidea, in my opinion, indicate that this superfamily should be set apart from the rest of the Heteroptera. I would suggest that it be placed in a division of equal status with the Pentatomomorpha.

Owing to the reduced nature of the female genitalia of the " Incertae sedis II ", no attempt has been made to place these families in the systematic arrangement.

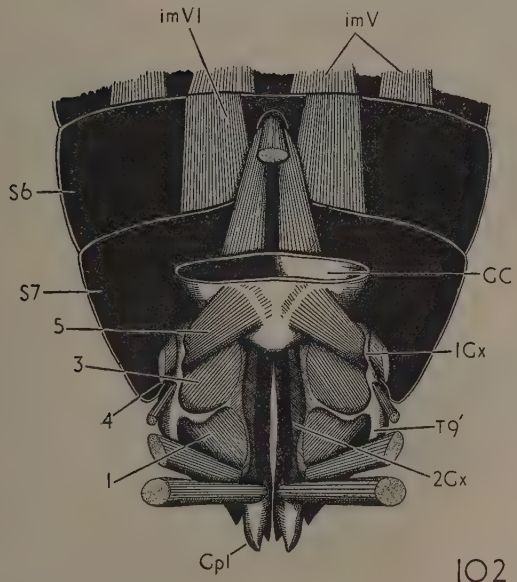
VIII Summary

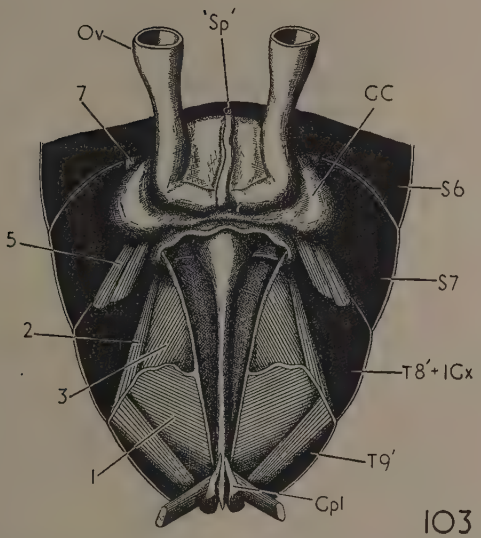
The structure of the female terminalia in the Heteroptera has been studied and their value in the systematics of the group is considered.

The current classification into families and superfamilies is supported, with few exceptions : *viz.* the family Stenocephalidae is distinct from the Alydidae and close to the Lygaeidae ; the Cydnid subfamily Coriomelaeinae and the Scutellerid subfamily Pachycorinae are perhaps heterogeneous ; the Colobathristidae are very similar to the Coreidae, and the Thaumastocoridae and Vianaididae are placed in the Cimicoidea and Tingoidea, respectively. The Mesoveliidae appear close to the Saldidae.

In the higher classification of the Heteroptera, the female genitalia suggest that the superfamilies fall into two groups, these groups coinciding with the division based by Pruthi (1925) on the male genitalia. In this grouping the Pentatomoid superfamilies are placed together as the Pentatomomorpha and the Cimicoid superfamilies, together with the aquatic and semi-aquatic bugs, as the Cimicomorpha. It has been found that the structure of the salivary glands also supports this grouping.

It has not been possible to place the Leotichidae, Galgulidae and Helotrephidae in any of the known superfamilies, but all three have definite relationships with the aquatic bugs. A number of families, owing to their specialized nature





FIGS. 102–103.—Internal view of musculature of female terminalia of : (102) *Nabis limbatus* Dahl. (Nabidae) ; (103) *Leptopterna dolabrata* (L.) (Miridae).

and lack of an ovipositor, have not been placed at all in the present work. The structure of the female genitalia, and the many other peculiar characters of the Corixidae, suggest that the latter need a higher category of their own, perhaps on the same level as the Pentatomomorpha.

It is seen that in both the Pentatomomorpha and Cimicomorpha, the type of ovipositor is dependent on the oviposition site and habit. Those ovipositing in plant or animal tissue have a laciniate type of ovipositor with sclerotized, lanceolate blades and the anterior strut of the gonangulum heavily sclerotized. Those ovipositing on the surface of leaves, trunks, etc. have a plate-shaped type of ovipositor with membranous flap-like gonapophyses and the anterior strut of the gonangulum often membranous or completely absent.

IX. Acknowledgments

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XI. Key to Lettering of Figures

a.l, anal lid.
b, spermathecal bulb.
d.fl, distal flange.
DP, dorsal pouch.
fc, fecundation canal.
Ga, gonangulum.
GC, genital chamber.
Gpl, gonoplac.
im V, *im VI*, intersegmental longitudinal muscles of segments V and VI.
lm VII, lateral intrasegmental muscle of segment VII.
Ov, *ov*, oviduct.
p.fl, proximal flange.
ps, pseudospermatheca.
r.s, ring sclerite.
sac, ramal sac.
sd, spermathecal duct.
Sp, spermatheca.
"*Sp*", accessory gland (homologue of true median spermatheca).
S6, *S7*, *S10*, Sterna VI, VII, X.
T8, *T9*, terga VIII and IX.
T8', *T9'*, paratergites VIII and IX.
X, segment X.

1Gpo, *2Gpo*, first and second gonapophysis.
1Gx, *2Gx*, first and second gonocoxa.
1, extensor muscle of gonapophysis (homologous to 29 IX in Scudder, 1959).
2, posterior dilator muscle of genital chamber.
3, retractor muscle of second gonapophysis (homologous to 28 IX in Scudder, 1959).
4, tergal muscle of first gonocoxa (probably homologous to 28 VIII in Scudder, 1959).
5, anterior dilator muscle of genital chamber.
6, retractor muscle of first gonapophysis (homologous to 14 VIII in Scudder, 1959).
7, retractor muscle of first gonocoxa (homologous to 15 VII and in some cases, where two muscles are present, also to 14 VII in Scudder, 1959).

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